# A GEOMETRIC APPROACH TO MODELLING INTERACTING POPULATIONS

by

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### Abstract

The purpose of this thesis is to present a different approach to the formulation of differential equation mathematical models for interacting populations. It does this through considering a geometric method. The solution to the differential equations are forced, through their formulation, to lie on the surface of well known three-dimensional shapes. It is this that allows detailed analysis of how, and why, the solution of the equations behave as they do.

The thesis firstly reviews some of the skills and techniques used in the formulation and analysis of differential equation models to give a background for some of the analysis used in the geometric approach to modelling. The geometrical approach is then presented using two three-dimensional surfaces, the ellipsoid and the torus. Also examined is an extension of the basic shape to higher dimensions. Using the three-dimensional shape as a reference, a four-dimensional representation is formulated. This increase in the number of variables in the model allows more situations to be modelled.

The thesis concludes by discussing the use of the type of model produced by the geometric approach by addressing some of the advantages and disadvantages of this approach. It ends with some extensions to this study of geometric models for future work.

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Signed ..............................

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# Chapter 1

# Introduction and Literature Review

## 1.1 Introduction

Working with a mathematical modeller of marine ecosystems for a few months encouraged an interest in the formulation of such models. Many weeks were spent 'tweaking' parameter values in order for the model to fit the data. Changing one parameter caused the need to change another, then another and often the first one again. This frustrating aspect of model formulation lead to this study of a geometric approach to mathematical modelling. If the feeling of 'loss of control' over a model could be reduced in any way then that had to be a bonus. This thesis presents this approach in order to illustrate how to build geometrically based models for interacting populations and some of the possible outcomes of the solutions.

## 1.2 Thesis Outline

Chapter 2 introduces some of the skills and techniques used in the formulation of mathematical models. In Section 2.2 the steps of modelling are discussed in order to give a background for some of the analysis used in the geometric approach to modelling in the following two chapters. It examines how assumptions, simplifications and knowledge about population dynamics can be used effectively to build plausible models for many situations. The underlying mathematics behind any differential equation model and some mathematical procedures that help to build the model are discussed fully in Section 2.3. In Section 2.4 a few examples are examined that show this analysis in practice.

In Chapters 3 and 4, a new procedure is presented which removes some of the ambiguities that usually face the modeller of interacting populations. The method involves starting with solutions and working backwards to achieve the differential equations which form the basis of the model. This modelling process uses geometric shapes as bases for the model, it is relatively easy to obtain a set of differential equations from the equation of a surface. Chapters 3 and 4 examine two surfaces, the ellipsoid and the torus. Each surface produces a large set of possible three variable models, of which a few are discussed in detail in each chapter. Also examined is an extension of the basic shape to higher dimensions. Using the three dimensional shape as a reference, a four dimensional representation is formulated. This increase in the number of variables in the model allows more situations to be modelled. Three different models are examined for the four dimensional ellipsoid and one model for the torus.

Chapter 5, Evaluation of the Geometric Approach to Modelling, discusses the use of the type of model introduced in this thesis. It addresses some of the advantages of using a geometric approach over the traditional method of model formulation. No model, however detailed, is perfect and this geometric formulation is no exception. Therefore in this chapter there will be a discussion of the disadvantages of this approach.

Chapter 6 indicates some extensions to this study of geometric models for future work.

## 1.3 Literature Review

There are numerous text books covering the principles of mathematical modelling. Some approach the subject from a mathematical aspect giving examples from all branches of biology, physics, mechanics etc. (Bender, 1978, Cross and Moscardini, 1985, Edwards and Hamson, 1989 and the Open University course Modelling with Mathematics, 1985, are a few). They all give a good general introduction to the mathematics of modelling. Specific mathematical areas of modelling such as stability analysis and solving differential equations by numerical methods are covered widely from both a mathematical and ecological aspect in many books. A general introduction to stability analysis is given in the Open University's Modelling with Mathematics course and a more detailed approach from an ecological point of view is given in May, 1973, while Gantmacher, 1977, covers the necessary theory of matrices. The theory of differential equations is available in many mathematical books among which are Jordan and Smith, 1977, and Redheffer, 1992. Solving differential equations by numerical methods is covered by Hall and Watt, 1976, Lambert, 1973, and Powell, 1970. Since this thesis is concerned with possible ecosystems models attention was paid to mathematical modelling from an ecological perspective. Jeffries, 1989, Pielou, 1974, Pielou, 1977, Renshaw, 1991, and Rossenbrock and Storey, 1970, are a few of the books that tackle mathematical modelling from such an angle.

Many papers have been written that highlight the mathematics of modelling specific situations. There are also papers which purely present the model itself. Abrams, 1975, Guowei *et al*, 1991, Grammaticos *et al*, 1990, Hofbauer *et al*, 1987, May and Leonard, 1975, May, 1976, Murty and Rao, 1987, and Smale, 1976, are a few which describe mathematical processes such as differential equations, analytical solutions and coefficient choice with reference to well known dynamic systems such as the Lotka-Volterra system, logistic equations, and simple competition models.

Stability analysis is also discussed widely in papers on ecosystem modelling, for example

Alymkulov, 1991, Brauer, 1977, Goh, 1977, Grimm *et al*, 1992, Haydon, 1994, Moore *et al*, 1993, and Phillips, 1978. A paper widely quoted by many when discussing stability is a paper related to economics but deals specifically with the analysis of stability is Quirk and Ruppert, 1965.

The literature reviewed for this thesis is mainly concentrated on the mathematics behind differential equation models and on a few specific ecosystem models. In this way it has provided a very general background to the work in the main body of the thesis. This thesis covers a topic that has not been approached before and therefore is new and has no specific references typical of PhD theses. However the literature, both books and papers, proved very useful in providing, firstly, a good set of 'tools' with which to tackle the geometric approach, and, secondly, further reasons to justify such an approach in terms of usefulness. Many of the modelling papers followed the same modelling technique; formulate the equations, compare with reality, tweaking the parameters to fit the data provided. Such modelling techniques often lead to a feeling of detachment from one of the main principles, a thorough understanding of the mathematics and the implications of any changes that are made to any of the parameters in the model. The aim of the thesis is to provide a different approach to mathematical modelling via a more structured method. This approach leads to a greater control over any particular model.

# Chapter 2

# An Introduction to Mathematical Modelling

## 2.1 Introduction

This chapter of the thesis introduces the ideas behind mathematical modelling. In Section 2.2 the steps of modelling are discussed in order to give a background for some of the analysis used in the geometric approach to modelling in the next two chapters. It examines how assumptions, simplifications and knowledge about population dynamics can be used effectively to build plausible models for many situations. The underlying mathematics behind any model and some mathematical procedures that help to build the model are discussed fully in Section 2.3. In Section 2.4 a few examples are examined showing the analysis in practice.

## 2.2 The Steps in Model Building

### 2.2.1 Introduction

Time related mathematical models are the translation of real situations into equations. These equations are then solved to give a value to each variable being examined at different times. Thus from the solutions a picture can be built up to see how the model predicts the changes in each variable over time. If this picture matches how the variables behave in real life then the model is accurate. However, no model will match field data exactly, no matter how sophisticated it is. It is virtually impossible to be 100% reliable when collecting any field data; for example several readings are usually taken at one place or time and then averaged; humans and machines make errors; the natural environment is infinitely variable, the causes of errors in data are numerous. It is deciding when the model is *close enough* to the data that causes problems when validating models; how close is close enough?

Mathematical modelling is a cyclic process, a good modeller should appreciate the need to go round the cycle a number of times before the model produced is acceptable. This cyclic nature of modelling is summarised diagrammatically below, Open University, 1985.

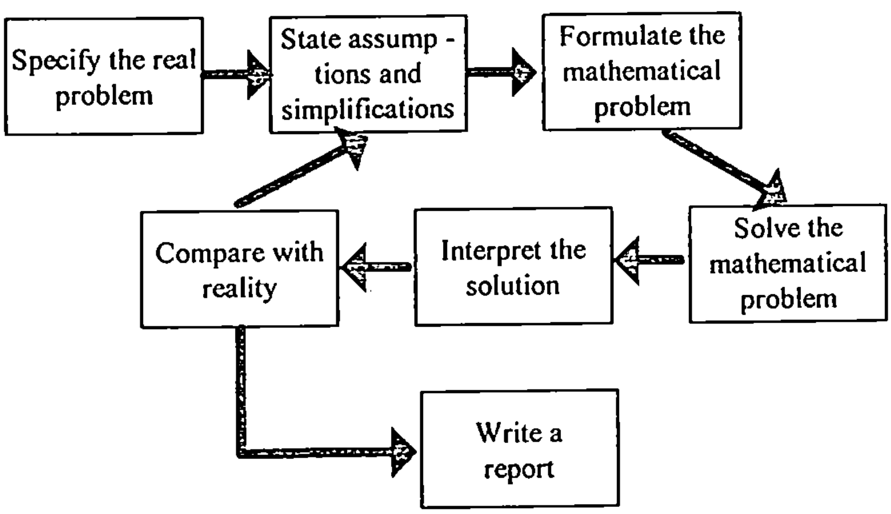


Figure 2.1: The mathematical modelling cycle

Once the real problem has been specified there are three distinct stages to the building of mathematical models. They are i) assumptions and simplifications, ii) the interpretation of the real situation by or through mathematics and iii) the validation of the model. The validation stage compares how well the model fits the situation being modelled. If, through comparison, the modeller discovers that the model is not behaving as was expected then the previous stages need to be examined again and improved on and the cycle repeated.

It is the first stage i.e. the simplifying assumptions that form the basis for any model. It would be impractical and unachievable to include *all* the information as to why certain variables behave as they do, especially when considering living organisms or ecological effects. Assumptions and simplifications are needed in order to formulate a usable model, the key being the ability to simulate often highly sophisticated situations whilst at the same time preserving important aspects of reality. With today's use of powerful computers the move appears to be towards building more and more sophisticated models without realising that the simpler models remain useful. Much can be learnt by making some assumptions and simplifications which result in models where mathematics can be more easily understood and interpreted. Much less can be learnt from large sophisticated models that contain too much information to make sense of the processes by which they work.

It can be concluded therefore that a good modeller creates models containing as much of the fundamental knowledge of the situation as possible whilst at the same time keeping them simple enough to interpret. The motto of every modeller should be William of Occam's (*ca* 1290-1350) words: *"It is vain to do with more what can be done with fewer"*, Russell, 1947.

### 2.2.2 Assumptions and Simplifications

According to Bender, 1978, when trying to model reality the world is divided into three parts: the unimportant, the exogenous and the endogenous i.e. the components whose effects can be neglected, the components that affect the model but whose behaviour the model is not designed to study and the components whose behaviour the model is designed to study. It is deciding what is unimportant enough to be neglected and the exogenous effects of the variables that are the assumptions. Everyone agrees that the model must be kept as simple as possible, especially on its first formulation (Bender, 1978, Cross and Moscardini, 1985, and Edwards and Hamson, 1989, for example). It is therefore a balance between simplicity and achieving realism. Levins, 1968, notes that "it is not possible to maximize simultaneously generality, realism and precision". Often the decision on what to neglect can be made a little easier by detailing for whom and for what the model is intended. A social scientist is often satisfied with much general results i.e. things increase or decrease and so in this instance, precision will therefore give way to realism and generality, (Bender 1978). Models which are built to simulate specific systems aim for precision and realism but end up being limited in their generality. Therefore general models may sometimes contain more information than specific ones in order to cover different circumstances. The skill of the modeller lies in deciding what factors are important as well as having a detailed understanding of the exogenous effects i.e. how the factors included in the model interact with each other.

Often, however, the modeller may not know how the factors being modelled behave in relation to each other so this stage also incurs assumptions and simplifications. For example the well known Lotka–Volterra model of a predator prey system, (Edwards and Hamson, 1989, Pielou, 1977), assumes that the rate of predation is proportional to the numbers of encounters between the prey and its predator. For the first formulation of the model such a simplification of reality may be feasible. However if the modellers found that their results were not fitting reality then it may mean that they have over-simplified matters.

This step of model building will therefore prove the skill of the modeller. Whether the final model is a success or failure relies heavily on the assumptions and simplifications made before the mathematics are even considered. As Edwards and Hamson, 1989, observe "to be a successful mathematical modeller it is not sufficient to have expertise in the techniques of mathematics, statistics and computing". They include other attributes as clear thinking, a logical approach and enthusiasm. The need to return a number of times to examine and improve the assumptions and simplifications definitely requires patience and an open mind as well as mathematical skills.

### 2.2.3 The Translation into Mathematics

There are two different types of models; deterministic and stochastic. Edwards and Hamson, 1989, describe deterministic models as those "usually used in cases where the outcome is a direct consequence of the initial conditions of the problem" and stochastic models for "those situations where a random effect plays a central role in the problem". Many modellers tend to use only one or the other but as Renshaw, 1991, points out "slavish obedience to one specific approach can lead to disaster" and suggests that both approaches should be employed simultaneously. However, having said that, this thesis will concentrate wholly on the deterministic model and on one type only, the differential equation model. This is the mathematical model most widely used by mathematicians and scientists although the difference model is sometimes employed.

#### 2.2.3.1 Differential Equations

Many models, especially those concerned with ecological and biological processes, involve time and the modeller is concerned with the problem of describing how the variables being studied are affected as time progresses. Therefore rates of change of the variables with time need to be studied and thus the differential equation model is formulated. This is done by considering the changes that occur in the variable over a finite but small time interval $\Delta t$. To obtain finite rates of change the expression is divided by $\Delta t$, the differential equation is obtained by then taking the limit as $\Delta t$ tend to zero. As the modeller becomes more adept he or she will have no need for this process and will be able to formulate the change in variables simply as differential equations. However it is still a useful tool to be able to work from first principles and an example is given below to illustrate the procedure.

This example concerns a model for the population growth of a single species, Edwards and Hamson, 1989. The size of the population is required to be known at any time. It is assumed that the size of the population is defined as the total number of living individuals, taking no account of age, gender etc. Another assumption which is necessary in order to formulate a differential equation model is that this total number is a continuous variable $P(t)$. Obviously population size is a discrete variable but if the time step is very small "a graph with very small discrete steps will be indistinguishable from a smooth curve." This is an assumption employed by all modellers who use differential equations to model discrete variables.

Next, the reasons for what causes a population to change over time need to be examined. Obvious changes in the size of the population occur when individuals are born or die. Other changing factors could be emigration or immigration. These words need to now be translated into mathematics. To start, an equation reflecting the change in the size of the population over a small time period $\Delta t$ is proposed. In words the equation would therefore be as follows:

$$\begin{aligned}\begin{pmatrix}\text{Increase in population}\\ \text{during time } \Delta t\end{pmatrix} &= \begin{pmatrix}\text{Births during}\\ \text{time } \Delta t\end{pmatrix} - \begin{pmatrix}\text{Deaths during}\\ \text{time } \Delta t\end{pmatrix}\\ &+ \begin{pmatrix}\text{Immigration during}\\ \text{time } \Delta t\end{pmatrix} - \begin{pmatrix}\text{Emigration during}\\ \text{time } \Delta t\end{pmatrix}.\end{aligned}$$

To illustrate the principle the model is kept as simple as possible and so immigration and emigration are ignored for this example. The number of births and deaths will depend on the size of the interval $\Delta t$ and the size of the population at the beginning of the time interval. Assuming that the number of births and deaths are strictly proportional the words can now be translated in to mathematics as follows:

$$\text{number of births in the time interval} = BP(t)\Delta t,$$

$$\text{number of deaths in the time interval} = DP(t)\Delta t$$

where $B$ and $D$ are parameters i.e. the rate at which the births and deaths occur.

Therefore a model to show the change in population size after the time interval $\Delta t$ is

$$P(t + \Delta t) - P(t) = (B - D)P(t)\Delta t. \tag{2.1}$$

To represent Equation 2.1 as a differential equation it is rearranged as

$$\frac{1}{P(t)} \frac{P(t + \Delta t) - P(t)}{\Delta t} = B - D. \tag{2.2}$$

Letting $\Delta t \rightarrow 0$ Equation 2.2 becomes

$$\frac{1}{P(t)} \frac{\mathrm{d}P(t)}{\mathrm{d}t} = B - D \tag{2.3}$$

and the model is therefore

$$\frac{\mathrm{d}P(t)}{\mathrm{d}t} = (B - D)P(t). \tag{2.4}$$

The left hand side of Equation 2.3 is called the proportionate growth rate and in this case the proportionate growth rate is a constant, namely $B - D$. If $B - D > 0$ the population is increasing, if $B - D < 0$ then the population is decreasing.

This extremely simplified model is totally unrealistic because it predicts that the size of the population will grow exponentially without limit if $B > D$ and this very rarely happens in practice. By changing the proportionate growth rate the modeller can incorporate different effects into the model. For example, in order to build into the above model effects of limited food or space then a choice of the proportionate growth rate is chosen so that as the population size increases its growth rate decreases. Such a choice could be

$$\frac{1}{P} \frac{\mathrm{d}P}{\mathrm{d}t} = \alpha - \beta P \tag{2.5}$$

where $\alpha$ and $\beta$ are parameters. (Note that parameters in models are always positive; they are either added or subtracted from the equation to indicate growth or decay.) Therefore the model in this case is

$$\frac{\mathrm{d}P}{\mathrm{d}t} = P(\alpha - \beta P). \tag{2.6}$$

Even though basic simple models can be written in terms of the proportionate growth rate for each variable, the more sophisticated ones will include terms preventing this representation.

Usually models involve many variables and so sets of coupled differential equations are needed. Each equation is expressed in terms of all or some of the other variables in the model depending on how they effect each other.

The general form of the equations are:

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = f_i(x_1, x_2, \ldots, x_n) \tag{2.7}$$

where $n$ is the number of variables in the model, $i = 1, 2, \ldots, n$, $x_i$ represents the size of population $i$ at time $t$ and $f_i$ is a function of all the terms which govern the changes in population $i$.

The extremely simple Lotka–Volterra predator prey model which is discussed fully later in this chapter (Section 2.4) is governed by following set of differential equations:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = a_1 x - b_1 xy, \tag{2.8a}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = -a_2 y + b_2 xy \tag{2.8b}$$

where $x$ and $y$ represent the size of the prey and predator populations respectively and $a_1$, $b_1$, $a_2$, and $b_2$ are parameters.

It has been assumed that the prey gets eaten only by this one predator, the prey's food is abundant and the predator eats only this one species of prey. The change in the size of the prey population due to births and natural deaths is represented by $a_1 x$ and the change due to predation by the term $-a_1 xy$. As mentioned before, the assumption that this change is proportional to the numbers of encounters between the two species is employed. Similarly the changes in the population size of the predator are translated as the terms $-a_2y$ and $b_2xy$ i.e. the births and natural deaths of the predator and the increase due to the predation.

The above two examples give some idea of how words can be translated into mathematics. However there are no hard and fast rules when modelling. It may sometimes be a failing of a modeller to be unwilling to accept that the same situation can be translated into mathematics in a number of ways. As Edwards and Hamson, 1989, say "Many different models can be developed from tackling the same problem" and that "the same abstract model can often be used for quite different physical situations".

They also point out that the first step when trying to write down the relevant differential equation is to state the obvious. Most differential equation models are based on the 'input–output' principle:

$$\begin{pmatrix} \text{Net rate} \\ \text{of change} \end{pmatrix} = \begin{pmatrix} \text{Rate of} \\ \text{input} \end{pmatrix} - \begin{pmatrix} \text{Rate of} \\ \text{output} \end{pmatrix}.$$

Remembering this obvious but important principle will assist the modeller in this stage of the model building.

#### 2.2.3.2 Parameter Values

Once the model has been formulated the task of putting values to the parameters must begin. If the model is built to simulate data then different parameter values can be tried until the model fits the data. Therefore this part of the process is also linked to the validation stage.

It is usual for models to contain information from previous models in the way of parameters for certain processes. What may be correct for one situation may however not be suitable for another. The original model may be based on data which was specific for a certain date or place and it is not really wise to assume that it is typical of all situations. However such an approach is valid if the modellers use their previous knowledge wisely before launching into a new model.

Therefore this part is one of logical guesses and familiarity with similar situations. For example, in the Lotka–Volterra model (Equations 2.8) there are four parameters to find; the natural birth and death rates of the prey and the predator, $a_1$ and $a_2$, the death rate of the prey due to the predator, $b_1$, and the growth rate of the predator due to its predation on the prey, $b_2$. In this situation it is reasonable to presume that $a_1$ is going to be larger than $a_2$ due to the fact that the prey is usually smaller and therefore will have a faster growth rate than the larger predator. Similarly it is acceptable that $b_1$ is larger than $b_2$ on the basis that many of the prey will need to be consumed by the predator to increase its growth rate. Therefore it can be seen how logic and intelligent guesses play their part. It will be pointless allowing parameter values to take on any value just to fit the data. If a stage is reached where the modeller finds himself allocating a nonsensical value to a parameter then the formulation of the model i.e. the assumptions and simplifications need to be re-examined.

Unfortunately there are no hard and fast rules concerning parameter values apart from those whose value is fixed or must be in a certain range. There may be some cases when the modeller wishes the model to behave in a specific way and then the parameter values will play a part in this. The role that the parameters may play is discussed in Section 2.3.2.

### 2.2.4 Solving Differential Equations

The next step in the model building process is the solving of the mathematical problem. Solving systems like those above is usually a straight forward affair of simple integration. For example Equations 2.4 and 2.6 are integrated to give the function $P(t)$ in terms of the time $t$:

$$P(t) = P(0)e^{(B-D)t} \tag{2.9}$$

and

$$P(t) = \frac{M}{1 + (\frac{M}{P(0)} - 1)e^{(-\alpha t)}} \tag{2.10}$$

respectively where $P(0)$ is the population size at time $t = 0$ and $M = \alpha/\beta$, known as the carrying capacity of the population.

With two or more variables it is not always possible to obtain a solution for each variable in terms of $t$. For the predator prey model above Equations 2.8 can be rewritten as

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{y(b_2x - a_2)}{x(a_1 - b_1y)} \tag{2.11}$$

and so

$$\begin{aligned}
(\frac{a_1}{y} - b_1)\mathrm{d}y &= (b_2 - \frac{a_2}{x})\mathrm{d}x && (2.12)\\
a_1\ln(y) - b_1y &= b_2x - a_2\ln(x) + c && (2.13)
\end{aligned}$$

where $c$ is the constant of integration. It is possible to obtain $x$ and $y$ in terms of $t$ but only in a limited region. (This will be shown when this model is discussed further in Section 2.4.) However a general solution can not be found even for this simple model. Since many models are much larger and more sophisticated than then this simple model, modellers do not attempt to solve them explicitly in terms of time.

Numerical methods for solving differential equations exist which calculate the value of each variable at given time steps. Therefore a solution curve in the shape of a time series plot can be obtained instead. However it must be remembered that all numerical methods are approximations and so care must be taken when employing such methods to ensure accuracy and to minimise errors. With today's computers this is less of a problem than it was when modellers relied on calculators and reams of paper although the old adage must still be remembered: garbage in; garbage out! Details of the numerical methods are not given in this thesis as there are numerous text books describing the methods. (Hall and

Watt, 1976, Jordan and Smith, 1977, Lambert, 1973, and Redheffer, 1992, are a few). The modeller must be a competent computer programmer but since there are ready written routines for the integration the details are not relevant. The fourth order Runge–Kutta–Merson method (Hall and Watt, 1976), which is available as a NAG subroutine (D02BBF) for FORTRAN has been used to integrate all the models in this thesis. Details are given in Appendix C.

### 2.2.5 Validation

Validation is the step in the model building process which gives an indication of how well a fit the model is to real life. It can either be the final stage in the modelling process or the one that shows the previous steps need to be revised, most often it is the second of these. That is why most data based modelling processes tend to be cyclic; from comparing the model results with the real information the modeller can see where the assumptions have broken down and can get an indication of which parameter values give better fits to the data. Therefore the validation stage is a checking stage for the work done in formulating the model.

Part of the validation process is an analysis of how the model is actually behaving and deciding if such behaviour is typical of the situation trying to be modelled. The first run of the modelling process may have over–simplified the situation and therefore produce an unrealistic model. There are several mathematical tools which can be employed by the modeller to assist in this task and they are considered in some depth in the following section (2.3). A model is valid only if it correctly and accurately describes the situation being considered.

The main part of model validation is comparing model results with data. One of the main problems with this is that the modeller must rely on the data being accurate. If the model fits the data almost perfectly but however the data itself is inaccurate then the model is not a true representation of the processes being examined. Models based on data are therefore at most only as good as the data. The problems associated with data and how data should be used to obtain accurate models is discussed in Section 2.3.3

## 2.3 Some Mathematical Tools of Model Building

### 2.3.1 Introduction

A number of methods and procedures that will help the modeller to improve the model and its validation are discussed in this section. The part on stability analysis (2.3.2) deals in some detail on how such analysis can be used to understand how a model behaves. Knowing the behaviour of a model can allow assumptions and simplifications to be justified or not as the case may be. Such analysis can also help in the task of assigning values to the parameters in the model. The part on data based models (2.3.3) investigates how an understanding of data can help in both the formulation of a data based model and its validation.

### 2.3.2 Stability Analysis

#### 2.3.2.1 Fixed Points of Systems

A 'fixed point of a system' occurs when there is no change in the values of any of the variables i.e. in population terms, population sizes are neither increasing or decreasing. Obviously such points occur when all $\frac{dx_i}{dt} = 0$, $i = 1 \ldots n$ where each $x_i$ is a variable in the model. For simple small models these points can easily be found, for more sophisticated systems numerical analysis is required and computer algorithms can be implemented to find the fixed points of any size system of equations, (Powell, 1970). The one used in this study has been the NAG routine C05NBF for FORTRAN. See Appendix C for details.

### 2.3.2.2 Types of Fixed Points

Fixed points can be classified by the behaviour of the variable near the point. If the solution to the differential equations *converges* towards the fixed point as time progresses then that point is classified as a *stable fixed point*. If the solution *diverges* from the point then the point is classified as an *unstable fixed point*. If the solution *oscillates* around the point without ever reaching it then that type of point is known as a *centre*. There are also fixed points which are classified as *semi-stable*. The behaviour of such points depends on the direction of approach; if the solution curve approaches the point from one direction it will behave in the manner of a stable fixed point, if the solution curve approaches the point from the other direction it will behave in the manner of an unstable point. Thus more detailed examination of the behaviour of the solution curves on either side of the point is required in this case.

Therefore generalizing the situation: An $m$ variable model is given by

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = F_i(N_1, N_2, \ldots N_m) \tag{2.14}$$

where $i = 1 \ldots m$, $N_i(t)$ represents population $i$ at time $t$, and $F_i$ is a function of the terms which govern the changes in population $i$. Let the fixed points of Equation 2.14 be $N_i^*$ and they are found by solving $\frac{\mathrm{d}N_i}{\mathrm{d}t} = 0$, $(i = 1 \ldots m)$, simultaneously.

Expanding the functions $F_i$ close to the fixed points $N_i^*$ using a Taylor expansion for $i = 1$ the following equation is found

$$\begin{aligned} F_1(N_1, N_2, \ldots, N_m) \;=\; & F_1(N_1^*, N_2^*, \ldots, N_m^*) \\ & +(N_1 - N_1^*)\frac{\partial F_1}{\partial N_1}(N_1^*, N_2^*, \ldots, N_m^*) \\ & +(N_2 - N_2^*)\frac{\partial F_1}{\partial N_2}(N_1^*, N_2^*, \ldots, N_m^*) + \ldots \\ & +(N_m - N_m^*)\frac{\partial F_1}{\partial N_m}(N_1^*, N_2^*, \ldots, N_m^*) \end{aligned} \tag{2.15}$$

$$+\mathrm{O}(N_1 - N_1^*)^2 + \mathrm{O}(N_2 - N_2^*)^2 + \ldots + \mathrm{O}(N_m - N_m^*)^2$$

$$+\mathrm{O}(N_1 - N_1^*)^3 + \mathrm{O}(N_2 - N_2^*)^3 + \ldots + \mathrm{O}(N_m - N_m^*)^3$$

$$+\ldots$$

where O represents terms 'to the order of'. Now $F_i(N_1^*, N_2^*, \ldots, N_m^*) = 0$ so to first order Equation 2.15 becomes in general

$$F_1(N_1, N_2, \ldots, N_m) = \sum_{i=1}^{m}(N_i - N_i^*)\frac{\partial F_i}{\partial N_i}(N_1^*, N_2^*, \ldots, N_m^*). \tag{2.16}$$

Now from Equation 2.14

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = F_i(N_1, N_2, \ldots, N_m) \tag{2.17}$$

where $(N_i - N_i^*) = x_i$. Therefore

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = \sum_{j=1}^{n} x_j \frac{\partial F_i}{\partial N_j}(N_1^*, N_2^*, \ldots, N_m^*) \tag{2.18}$$

which can be written in matrix form as

$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \vdots \\ \dot{x}_m \end{bmatrix} = \begin{bmatrix} \frac{\partial F_1}{\partial N_1} & \frac{\partial F_1}{\partial N_2} & \cdots & \frac{\partial F_1}{\partial N_m} \\ \frac{\partial F_2}{\partial N_1} & \frac{\partial F_2}{\partial N_2} & \cdots & \frac{\partial F_2}{\partial N_m} \\ & \vdots & & \\ \frac{\partial F_m}{\partial N_1} & \frac{\partial F_m}{\partial N_2} & \cdots & \frac{\partial F_m}{\partial N_m} \end{bmatrix}_{N_1^*, N_2^*, \ldots, N_m^*} \begin{bmatrix} x_1 \\ x_2 \\ \vdots \\ x_m \end{bmatrix} \tag{2.19}$$

i.e.

$$\dot{\underline{x}} = \mathbf{J}\underline{x} \tag{2.20}$$

where J is known as the Jacobian matrix. It is the eigenvalues of J which determine the behaviour of the fixed points and thus that of the entire system.

The eigenvalues $\lambda_j$ are found from the equation

$$(\mathbf{J} - \lambda_j \mathbf{I}) = 0. \tag{2.21}$$

Equation 2.21 possesses a non-trivial solution if $|\mathbf{J} - \lambda_j \mathbf{I}| = 0$ and the solutions are in the form of an $m$th order polynomial in $\lambda$,

$$a_0\lambda^m + a_1\lambda^{m-1} + a_2\lambda^{m-2} + \ldots + a_m = 0 \tag{2.22}$$

with the general form of $\lambda$ being a complex number $\lambda = \mu + i\omega$ $(i = \sqrt{-1})$.

So the general solution of Equation 2.18 is

$$x_i(t) = \sum_{j=1}^{m} c_{ij} e^{\lambda_j t} \tag{2.23}$$

where $c_{ij}$ are parameters. This indicates that the real part of $\lambda$ (i.e. $\mu$) produces exponential growth or decay and the imaginary part ($\omega$) produces sinusoidal oscillations. It is the sign of $\mu$ which determines the type of fixed point.

If the real part of $\lambda$ is negative (i.e. causing exponential decay) then the difference between the solution and the fixed point will become less and less with each time step. The population will therefore eventually settle down to that fixed point. So if the eigenvalue corresponding to that fixed point has *negative real part* then the fixed point is classified as a *stable fixed point.*

If the real part of $\lambda$ is positive then the exponential factor increases with time causing the difference between the solution and the fixed point to increase with time. This means that the population never settles down to the fixed point but moves away from it. So if the eigenvalue has *positive real part* then the fixed point is classified as an *unstable fixed point.*

If the eigenvalue has zero real part then the sinusoidal part of $\lambda$ remains and so the population will oscillate around the fixed point continually. So if the eigenvalue has *zero* *real part* then the fixed point has *neutral stability* and is classified as a *centre*.

Sometimes the solution of the polynomial in $\lambda$ will result in two eigenvalues for $\lambda$ with different signs. In this case the fixed point will be *semi-stable* and the behaviour of the solution curves either side of the point need to be examined in more detail.

Some systems may have more than one fixed point and therefore the above analysis will need to be carried out for each fixed point. Therefore, since the fixed points of the system depend on the values of the parameters in the differential equations, by examining the stability of the system some conditions for these parameters may be found. One must build into the model the information one knows about the system. For example, if from the time series plots it can be seen that the populations seem to settle down to fixed levels then the fixed point of that system must therefore be stable. Once the basic model is built then the stability of the fixed point can therefore be guaranteed by ensuring that the eigenvalues of its Jacobian matrix have negative real parts. Consequently it would be useful if there was some way of determining if the eigenvalues have negative real parts, positive real parts or zero real parts. For small simple models it is relatively simple to calculate the eigenvalues, for larger systems numerical methods and computer algorithms can be employed such as the NAG routine for FORTRAN F02AFF, details of which is in Appendix C, which calculates all the eigenvalues of a real non-symmetric matrix by reduction to Hessenberg form, Wilkinson and Reinsch, 1971.

#### 2.3.2.3 Stable Models

For a system to be stable the eigenvalues $\lambda$ of J need to have negative real parts. This can also be interpreted as saying that the roots of the resulting polynomial in $\lambda$ must have negative real parts.

The Routh-Hurwitz criterion, Gantmacher, 1977, Quirk and Ruppert, 1965, states that the roots of the real polynomial

$$a_0 z^m + a_1 z^{m-1} + a_2 z^{m-2} + \ldots + a_m = 0 \qquad (a_0 > 0) \tag{2.24}$$

will have negative real parts if

$$|a_1| > 0, \quad \begin{vmatrix} a_1 & a_3 \\ a_0 & a_2 \end{vmatrix} > 0, \quad \begin{vmatrix} a_1 & a_3 & a_5 \\ a_0 & a_2 & a_4 \\ 0 & a_1 & a_3 \end{vmatrix} > 0, \quad \ldots \begin{vmatrix} a_1 & a_3 & a_5 & \ldots & 0 \\ a_0 & a_2 & a_4 & \ldots & 0 \\ 0 & a_1 & a_3 & \ldots & 0 \\ 0 & a_0 & a_2 & \ldots & 0 \\ & & \vdots & & \\ 0 & 0 & 0 & \ldots & a_n \end{vmatrix} > 0. \tag{2.25}$$

Now $a_i$, $i = 1, \ldots, m$, are in terms of the elements $j_{ik}$, $i, k = 1, \ldots, m$, of the Jacobian matrix which are themselves in terms of the parameters in the original differential equations. So there are conditions on the parameters if the system is to be stable.

The larger the model is, the more conditions on the coefficients $a_i$ there will be if stability is required. These conditions have been nicely summarised by May, 1973, for up to five variables. He points out that "no-one in their right mind is going to use (the theorem) for $n > 5$ anyway."

For the polynomial $\lambda^m + a_1\lambda^{m-1} + a_2\lambda^{m-2} + \ldots + a_m = 0$ the necessary and sufficient conditions to ensure all eigenvalues $\lambda$ to have negative real parts are

$$m = 2 \qquad a_1 > 0, a_2 > 0, \tag{2.26a}$$

$$m = 3 \qquad a_1 > 0, a_3 > 0, a_1 a_2 > a_3, \tag{2.26b}$$

$$m = 4 \qquad a_1 > 0, a_3 > 0, a_4 > 0, \tag{2.26c}$$

$$a_1 a_2 a_3 > a_3^2 + a_1^2 a_4, \tag{2.26d}$$

$$m = 5 \qquad a_i > 0 \; (i = 1,2,3,4,5), \tag{2.26e}$$

$$a_1 a_2 a_3 > a_3^2 + a_1^2 a_4, \tag{2.26f}$$

$$(a_1 a_4 - a_5)(a_1 a_2 a_3 - a_3^2 - a_1^2 a_4) > a_5(a_1 a_2 - a_3)^2 + a_1 a_5^2. \tag{2.26g}$$

Remember that these conditions are on the coefficients of the polynomial. To find conditions on the actual parameters in the model the appropriate Jacobian matrix needs to be found and from this, the polynomial needs to be derived. So it is possible to end up with some very complicated constraints on the parameters.

#### 2.3.2.4 Fluctuating Models

This is the case where the fixed point of the system is a centre. While stable populations settle down to a fixed point after some time, fluctuating populations are continually changing size with time but in a cyclic way. For example consider a population with a yearly cycle such as a phytoplankton species, Taylor *et al*, 1992. During the winter there is just enough light and nutrient to support a small phytoplankton population. As late spring approaches the light, temperature and nutrient content of the oceans are conducive to phytoplankton growth and we have what is termed the 'spring bloom'. However as the population increases, its demand on the nutrients, mainly nitrites, increases also. This causes the nitrite levels to fall in late summer which in turn causes the phytoplankton population to decrease. It continues to decrease until it is of a size which can be supported by the available light, temperature and nutrients. The system has gone full circle; the population will grow again in the spring and continue cycling in this manner.

The modeller trying to model this phytoplankton population then would need to build into the model the fact that the population is a cyclic one. This means that the fixed point needs to be a centre and so the eigenvalues associated with the fixed point should have zero real parts. A useful result is that *the eigenvalues of a skew symmetric matrix are purely imaginary*. Therefore if little is known about the populations being modelled apart from the fact that they are cyclic then the parameters can be chosen with the aim of obtaining a skew-symmetric matrix.

It is important to remember that these two rules concerning eigenvalues are sufficient but not necessary. It is possible to obtain imaginary eigenvalues without a skew-symmetric matrix and eigenvalues with negative real parts without obeying the Routh-Hurwitz criterion. However, modelling needs to start somewhere and if it is known that the populations are stable or cyclic then at least this gives a starting point, particularly if this is all that is known.

### 2.3.3 Data Based Models

Ideally for population models the modeller would require the data collector to count each individual member of the populations at required time intervals so the true population size is then known. In some situations this could be possible; the area which the model covers needs to be small enough to be observed in the practical sense and the individuals need to be large enough and stationary enough to be counted. This is easy to do in laboratory experiments where the population is contained within a small area and the situation is in controlled conditions. Nicholson's blowfly experiments are such examples, Nicholson, 1954. In order to exhibit the cyclic nature of the blowfly population he reared 20 generations of fly in the laboratory. This took about one year and every few days somebody had the task of counting the eggs and adult flies.

When it is not possible to measure the whole population then a *sample* needs to be taken. The sample must therefore be as true to the whole population as possible. In gathering a sample one really needs to know about the behaviour of the individuals in the population. If they tend to move around the area that is being sampled then care needs to be taken not to sample the same individuals more than once. If they tend to live in groups then one sample will show a high population whereas another will show a sparse population, many samples would need to be taken for the two to balance out. Outside influences will also bias a sample. For example, if the sample was taken in a polluted area then that sample would not be representative of the whole area. These are just a few of the problems in gathering data on which to base a model; they cannot all be solved and therefore one must hope that the assumptions that need to be made are viable and lead to realistic models.

The two examples below give situations when samples were used and the effectiveness of each sampling method is discussed. This is in no way intended as a criticism of any specific model; it is merely an attempt to highlight the problems involved when sampling.

#### 2.3.3.1 Canadian Lynx and Hare

Many modellers who wished to illustrate cycling within mammal populations based their models on the lynx and hare population of Canada, Elton and Nicholson, 1942, Maclulich, 1937. The data from which all the models derive was an *estimate* of the population sizes; it is based on the records of the Hudson Bay Company about its fur trade. It has been assumed that the number of animals in Canada is proportional to the number of furs that were returned and sold at auction each year. At first this data was thought to be ideal for modelling purposes; it had been collected over a long time period (1735–1939) and seemed representative of the true population sizes. It was only when the records were examined more closely and known facts about the hares and lynx were taken into consideration that the flaws in the data became apparent. Among other things it was discovered that there were two distinct periods in the life of the Hudson Bay Company. Before 1774 it was not responsible for the entire country, French traders had a monopoly in central Canada, and it was only in 1820 that the Hudson Bay Company collected furs from all over Canada, Akçakaya, 1992. So really only the data from 1820–1939 was representative of the true population. A model by Gilpin, 1973, was based on the whole data set and concluded that the only way in which the data could be interpreted was that the hares 'ate' the lynx possibly by passing a disease fatal to the lynx but nonfatal to the hares. Finnerty, 1979, later pointed out Gilpin's mistake of misusing data.

This data also illustrates the need for some background knowledge of the populations. The models produce time series for the number of animals in Canada in a certain year but the records were for the year in which the fur was sold. An estimate of the time delay was needed in order for the models to correctly follow the true pattern. It was also discovered that the lynx used to come into the traps in large numbers when they were starving giving a higher estimate for that time than what was necessarily true. Another source of bias was introduced by the prices the furs were fetching. Despite fluctuations in the selling price of the fur therefore influencing the number sold, the trappers were paid at the same rate for long periods, Akçakaya, 1992. So, when the prices were high, fewer were being sold than caught and since the records were for the number sold this obviously led to misleading results.

Even though the flaws in the data are widespread it continues to be used as a basis for models. This illustrates some of the problems facing modellers; even though the data is known to be incomplete or contain errors it is the best that is available. The resulting model then may draw completely the wrong conclusions as in the case above. The modeller needs to be aware of the fact that data collection, and the subsequent interpretation of it, is full of pitfalls and so one needs to tread carefully when making any claims.

#### 2.3.3.2 Marine Biomass

Other assumptions need to be made when creating models which examine populations of extremely small organisms. Many of the marine ecosystems models are based on the smallest plants and creatures in the oceans i.e. phytoplankton and zooplankton. Here we have not only the problem of obtaining a true measure of abundance from a sample but how to actually *count* the organisms in the sample. It is impractical (and impossible) to simply count the number of organisms and an alternative measure is needed to represent the abundance.

The main method of measuring phytoplankton biomass in a sample is to measure the chlorophyll *a* concentration of the sample. All phytoplankton contain chlorophyll; they are plants and therefore need chlorophyll to utilise carbon dioxide. The concentration of chlorophyll in a sample is easy to measure and is now widely used as a measure of phytoplankton biomass for example Bannister, 1974, and Taylor *et al*, 1992. However as with all estimation methods there are a number of problems associated with using pigment concentration to represent the phytoplankton biomass: phytoplankton consists of a number of different species and the chlorophyll concentration is species specific; older cells contain less pigment than younger ones; the amount of chlorophyll present in a cell depends on the light intensity and nutrients; it is only chlorophyll *a* that is measured although other pigments are present in phytoplankton and chlorophyll concentration and cell size are not always correlated.

Apart from the errors that the above introduce into the estimation, obtaining a sample and measuring the chlorophyll concentration have their own problems. One of the methods used to measure pigmentation is by fluorometry. Phytoplankton chlorophyll fluoresces at a known wavelength. Fluorometers measure the amount of light emitted from a sample which is proportional to the chlorophyll concentration which is in turn proportional to the phytoplankton biomass. One problem with this method is that other pigments in phytoplankton also fluoresce with a wavelength close to that of chlorophyll *a* so leading to misleading counts. Another disadvantage is in calibrating the fluorometer. At least every 30 minutes it needs to be recalibrated which involves extracting the chlorophyll from a sample which has passed through the fluorometer and the amount of chlorophyll determined colourimetrically i.e. by the amount of colour in the sample, Morris, 1983. It is not difficult to see that this method of measuring chlorophyll is prone to inaccuracies.

Zooplankton biomass is slightly easier to measure since zooplankton are usually larger than phytoplankton. They can be counted using a microscope or even the naked eye but usually are measured by volume; the sample is allowed to stand for a period of time and the sediment then measured. Again though, it is the collection of the sample which leads to errors being introduced into the measurements. The two most common ways of collecting a sample are by using a water bottle or by towing a net. The water bottle has the problem that it is prejudiced towards the smaller zooplankton i.e. those of size 10 – 100$\mu$m since abundance is inversely proportional to size. The netting method has the reverse problem. In order for water to pass through the net with constant speed then the mesh has to be large enough; about 100$\mu$m thus allowing some of the smaller zooplankton to escape. Also as the net becomes fuller then the passage of water through it is inhibited and so the volume of water from which the sample is taken is not constant. Despite the problems these methods are the only practical ways to measure such populations.

The above two examples show the problems associated with basing models on data and using that data to validate the models. It is up to the modellers to recognise the fact that the data they receive and base their models on may contain discrepancies. If they do and deal with the data sensibly then a good working model can be produced. However it is when the modellers are ignorant of the fact that data can be wrong that the problems occur.

#### 2.3.3.3 Interpreting Graphical Representation of Data

If the model is to be based on data the modeller needs to understand what is causing the data to behave as it does and then incorporate this into the model. Usually the data which he or she is presented with are lists of numbers, dates and times for numerous observations. The first step is to display the data graphically, usually in the form of time series plots. This gives an indication of what is actually occurring to the populations as time proceeds. By comparing the time series for each population within the ecosystem that is being examined the way all the individual species interact to form the one ecosystem can also be discovered.

The time series graphs give an instant picture of how the population varies with time. If it remains a constant size then obviously the time series should be a straight line parallel to the time axis. If the population size fluctuates with time then the corresponding plot would have peaks and troughs. From such a plot one can see immediately where the peaks occur. This is important when, for example, modelling marine plankton ecosystems since the large increase in phytoplankton biomass in the spring (the spring bloom) plays an important role in influencing the concentrations of oxygen and carbon dioxide in the seas, Taylor and Watson, 1990. The modeller has an idea of when the peak occurs from previous studies but needs to make sure that it occurs in the correct place in this data set. Therefore a quick look at the time series plots can give the modeller a starting point; if the population size remains constant then the differential equation in the model for that species must be have a right hand side that is constant, if the population size fluctuates then that must be built into the model.

One of the major aims of producing models is to understand how different species in an ecosystem interact with each other. From the raw data the effects of this interaction might not be obvious. The time series plots therefore need to be examined in conjunction with each other and the patterns observed. If a trough in the distribution of one species follows a peak in another then it may be that predation or competition is occurring between the two. If two peaks occur at the same time then the populations may be symbiotic with each other or both feed of the same food which is plentiful. One population growing as the other decreases indicates a predation effect with the prey being consumed faster than it can be replenished. All the interactions therefore need to be noted, and with the help of previous knowledge need to decide which are actually interactions between population, which are just coincidence and which are merely errors in the data.

By plotting the data any unusual data points can be noted. These unrepresentative, rogue or outlying observations are a concern to those trying to interpret the data. Barnett and Lewis, 1978, define an outlier as "an observation (or subset of observations) which appear to be inconsistent with the remainder of that set of data". Such data points will arise in any data set, they can be human error, machine error or simply unusual circumstances at the time of data collection. These will show up on a plot of the data and then the modeller can decide what must be done about them.

#### 2.3.3.4 Dealing With Errors in Data

As mentioned above the data on which the model is to be based is bound to contain some outlying values, i.e. values inconsistent with the rest of the data. One of the modeller's main tasks is to decide which data gives an accurate picture of the situation and which is simply misleading. If the observations are truly errors then their inclusion in the data will cause difficulties in representing a true picture of the population. If the data is used to estimate the parameters for the model then the outliers will contaminate these estimates. Some errors may be mistakes in recording and examination of the raw data may give an indication of what the value should have been, a missing decimal point for example. Others however may have no obvious explanation and the modeller must decide first if it is actually a spurious point and secondly what to do about it. There are many statistical methods for determining whether a point is an outlier but these rely on underlying knowledge of the statistical distribution of the population, Barnett and Lewis, 1978, give full details. However raw data of ecological populations rarely follow neat statistical distributions and so these tests are of no benefit here. Normally it is left to the discretion of the modeller and his or her instincts.

Normally the modeller will simply discard the outlying value unless they have means for deciding what it should be, for example, in the case of mistakes in reading decimal points. They then face the risk of throwing away a potentially important point which could give a greater insight into why the population behaves as it does. This is one of the pitfalls of modelling with data. Until the time comes when the modeller is 100% certain that all the data is correct then this ambiguity over the validity will remain.

### 2.3.4 Statistical Methods for Validation

Often the only form of validation that takes place between a model's output and data is the unscientific method of "eyeballing", Dyke, 1996. The differences between the output and the data are compared and it is up to the modeller's judgement as to whether the model does predict how the data is behaving. However, there are various statistical tests which do compare differences which with today's computing facilities are not too difficult or time consuming to implement.

One is the $\chi^2$ hypothesis test which sets as its null hypothesis that there are no differences between the two sets of data. It uses as its test statistic the function

$$\chi^2 = \sum_{i=1}^{n} \frac{(\mathrm{O}_i - \mathrm{E}_i)^2}{\mathrm{E}_i} \tag{2.27}$$

where O represents observed values, E represents expected values and $n$ is the number of data points being tested. For this test the model output will have to produce a value corresponding to each data point i.e. the same time or position. This test can be used as follows. If the observed values are the measured data and the expected values are the model output then the procedure tests the null hypothesis that the model fits the data. The $\chi^2$ test statistic is then said to have come from a $\chi^2_{(n-1)}$ distribution if the null hypothesis is correct. Comparing the test statistic and the $\chi^2_{(n-1)}$ value at specified significance levels the hypothesis can be accepted or rejected. The disadvantage of this test is that the observed values must be greater than 5; if not then they are grouped into sets until they are. Obviously some models will be based on data which is small in magnitude and so this test will not be very much use then.

Other statistical tests are available but these tend to assume that the data has underlying statistical properties, e.g. comes from a Normal distribution. Most data will however not fit nicely into these specific categories.

## 2.4 Examples

In this final section on the mathematics of modelling some well known examples of ecosystem models are discussed in detail. The above tools are used to explore the nature of the system and how the models might be improved.

### 2.4.1 Predator-Prey System

This is a extremely simple model which is often used to illustrate certain principles of model building such as fixed points and stability, Edwards and Hamson, 1989, Pielou, 1977. It models a predator/prey or host/parasite situation and the first attempt building such a model should be one in which the simplest situation possible is assumed. For this first model the following simplifying assumptions are made.

- The prey gets eaten only by this one predator.
- The prey's food is abundant.
- The predator eats only this one species of prey

Next the 'function' for each species is decided. It must be a combination of all the effects that cause the population size to change. For the prey, it is obvious that its population size will *decrease* due to the predation by the other species. Another assumption that can be made here is that the rate at which the prey decreases due to the predation is proportional to the number of encounters between the two species. For such a simple model this is quite valid. Therefore the mathematical term corresponding to this decrease will involve a '$-xy$' term in the differential equation for the prey if $x$ is to represent the size of the prey population and $y$ is to represent the size of the predator population. Similarly it can be assumed that the predator population is going to increase due to its consumption of the prey and so there must be an '$+xy$' term in the differential equation for the predator. Now the prey population size must *increase* since one of the assumptions is that it always has enough food to maintain itself. Thus a further term in the prey equation will be an '$+x$'

term which takes into account the birth and natural death rate of the prey. Similarly, the predator population size will naturally decrease if there are no prey available and so an '$-y$' term is appropriate in the predator equation. These four terms can therefore describe how the two species behave. Each term is preceded by a parameter which is the *rate* at which each process affects the population size i.e. the rate at which the prey decrease due to the predation, the rate at which the predators increase due to the consumption of the prey, etc.

Therefore the differential equations which govern the changes in the two populations over time are given by

$$\frac{\mathrm{d}x}{\mathrm{d}t} = a_1 x - b_1 xy, \tag{2.28a}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = -a_2 y + b_2 xy \tag{2.28b}$$

where $a_1$, $a_2$, $b_1$ and $b_2$ are the parameters mentioned above. $a_1$ is the rate at which the prey population increases due to births and natural deaths, $b_1$ is the rate of interaction between the prey and the predator and so is proportional to the death rate of the prey due to being eaten by the predator, $a_2$ is the rate at which the predator population dies if there is no prey for it to feed on and finally $b_2$ is proportional to the rate of interaction between the predator and its prey and therefore is proportional to the rate at which the predator population grows from eating the prey. All the parameters will therefore be positive and their values need to be determined for each particular example of such a predator prey system.

By examining the stability of this system i.e. the eigenvalues of its Jacobian matrix it can be determined how it behaves and may be give some indication of relative values for the parameters. The fixed points of the system occur when

$$a_1 x - b_1 xy = 0, \tag{2.29a}$$

$$-a_2y + b_2xy = 0, \tag{2.29b}$$

The solutions to this set of equations are $x = 0$, $y = 0$ and $x = \frac{a_2}{b_2}$, $y = \frac{a_1}{b_1}$ giving two fixed points. It should be obvious that $(0,0)$ will be a stable fixed point; once both populations have died out they will remain in that state. At this stage however what occurs near to the other fixed point is less clear and so further investigation is required.

The Jacobian matrix corresponding to equations 2.28 is

$$\mathbf{J} = \begin{bmatrix} a_1 - b_1y & -b_1x \\ b_2y & -a_2 + b_2x \end{bmatrix}. \tag{2.30}$$

This matrix is then evaluated at each of the fixed points and so at the point $(0,0)$ the matrix 2.30 becomes

$$\mathbf{J} = \begin{bmatrix} a_1 & 0 \\ 0 & -a_2 \end{bmatrix}. \tag{2.31}$$

The eigenvalues of $\mathbf{J}$ occur when $|\mathbf{J} - \lambda\mathbf{I}| = 0$. The resulting polynomial in $\lambda$ is

$$\lambda^2 + (a_2 - a_1)\lambda - a_1a_2 = 0 \tag{2.32}$$

and so $\lambda = a_1$ or $\lambda = -a_2$. So in fact, the point $(0,0)$ turns out to be a semi-stable fixed point. However, it remains true to say that once both populations have died out they will not regenerate.

Evaluating $\mathbf{J}$ at the second fixed point $(\frac{a_2}{b_2}, \frac{a_1}{b_1})$ produces

$$\mathbf{J} = \begin{bmatrix} 0 & \frac{-b_1a_2}{b_2} \\ \frac{b_2a_1}{b_1} & 0 \end{bmatrix} \tag{2.33}$$

and the resulting polynomial from $|\mathrm{J} - \lambda \mathrm{I}|$ is

$$\lambda^2 = -a_1 a_2 \tag{2.34}$$

which has solutions

$$\lambda = \pm i\sqrt{a_1 a_2}. \tag{2.35}$$

Now $a_1$ and $a_2$ are positive parameters by their definition so therefore the eigenvalues are purely imaginary. Hence the fixed point $(\frac{a_2}{b_2}, \frac{a_1}{b_1})$ is a centre and the two populations are continually fluctuating around this point whatever the value of the parameters.

This fluctuation can be described in terms of the predator and prey interacting with each other. At a particular time there is a certain amount of each in the area being studied. The predator is eating its prey until the prey population begins to decrease. Now there is less around for the predator to eat and so that population will start to decrease. Now, with less predation the prey population can start to increase again. However this in turn leads to the predator population increasing; there is more for them to eat and the cycle begins again.

As mentioned in Section 2.24 it is possible to obtain equations for $x$ and $y$ in terms of $t$ but only 'near' to the fixed points. Let $X = x - \frac{a_2}{b_2}$ and $Y = y - \frac{a_1}{b_1}$ and therefore

$$\frac{\mathrm{d}X}{\mathrm{d}t} = a_1(X + \frac{a_2}{b_2}) - b_1(X + \frac{a_2}{b_2})(Y + \frac{a_1}{b_1}) \tag{2.36}$$

$$= -\frac{a_2 b_1}{b_2} Y - b_1 XY \tag{2.37}$$

and

$$\frac{\mathrm{d}Y}{\mathrm{d}t} = -a_2(Y + \frac{a_1}{b_1}) + b_2(X + \frac{a_2}{b_2})(Y + \frac{a_1}{b_1}) \tag{2.38}$$

$$= \frac{a_1 b_2}{b_1} X + b_2 XY. \tag{2.39}$$

Now since the fixed point is now the origin $XY$ can be considered negligible compared with $X$ and $Y$ near to the fixed point. Therefore Equations 2.37 and 2.39 can be approximated by

$$\frac{\mathrm{d}X}{\mathrm{d}t} = -\frac{a_2}{b_1}b_2Y, \tag{2.40a}$$
$$\frac{\mathrm{d}Y}{\mathrm{d}t} = \frac{a_1}{b_2}b_1X. \tag{2.40b}$$

Employing the same method as in Section 2.2.3.2 the above two equations can be rewritten as

$$\frac{\mathrm{d}X}{\mathrm{d}Y} = -\frac{a_2b_1^2}{a_1b_2^2}\frac{Y}{X} \tag{2.41a}$$

$$\int a_1b_2^2X\mathrm{d}X = \int -a_2b_1^2Y\mathrm{d}Y \tag{2.41b}$$

$$a_1b_2^2X^2 + a_2b_1^2Y^2 = c \tag{2.41c}$$

where $c$ is the constant of integration. Equation 2.41c is an equation of an ellipse and therefore 'near' the fixed point the $xy$ phase plane diagram will resemble an ellipse.

Therefore substituting for $X$ and $Y$ from Equation 2.41c into Equations 2.40 and integrating expressions for $x$ and $y$ can be found.

$$x = \frac{\sqrt{c}}{b_2\sqrt{a_1}}\cos(\frac{a_2}{b_2}t + \beta_1) + \frac{a_2}{b_2} \tag{2.42a}$$
$$y = \frac{\sqrt{c}}{b_1\sqrt{a_2}}\sin(\frac{a_1}{b_1}t + \beta_2) + \frac{a_1}{b_1} \tag{2.42b}$$

where $\beta_1$ and $\beta_2$ are parameters in the range $0 \leq \beta \leq 2\pi$.

Therefore near to the fixed point $x$ and $y$ behave in a sinusoidal manner. However this is only near to the fixed point, if the populations sizes are such that they are a long way from the centre then they will not conform to the above equations. However such analysis is useful in that it provides a starting point to see how the model behaves.

The next step in the modelling process is to designate some values to the parameters. If this model was based on data then from the time series plots it could be seen around what level the two populations are fluctuating. Therefore the modeller will have a good estimate for the fixed point. This means that there are only now two free parameters for which to find values since if $(x^*, y^*)$ is the fixed point then $a_1 = b_1 y^*$ and $a_2 = b_2 x^*$. Finding these requires some knowledge of the biology of the two populations as well as some logic.

By examining how each population behaves in the absence of the other it can help in finding a little more about the parameters. In the absence of any predators the change in the size of the prey population is

$$\frac{\mathrm{d}x}{\mathrm{d}t} = a_1 x \tag{2.43}$$

which integrates to

$$x = C_1 \mathrm{e}^{a_1 t} \tag{2.44}$$

where $C_1$ is the constant of integration. Hence the prey grow exponentially with time at a rate $a_1$. Similarly when there are no prey for the predator to survive on the change in the size of the predator population is

$$\frac{\mathrm{d}y}{\mathrm{d}t} = -a_2 y \tag{2.45}$$

and so

$$y = C_2 e^{-a_2 y} \tag{2.46}$$

where $C_2$ is the constant of integration. Hence the predator dies exponentially with a rate $a_2$. Now the modeller will have some idea of the biology of the two species and will know that the predator population dies at a slower rate than the prey population increases due to their relative size and so can assume that $a_1 > a_2$. Estimates of $a_1$ and $a_2$ can then be tried in the model to see which fit the data best. Figures 2.2 to 2.4 shows time series plots for the solution of Equations 2.28 for different starting points. Also shown in each case is the phase plane plot to show the cycling around the fixed point. It can be seen that the nearer the fixed point the population sizes are then the closer the phase plane becomes to an ellipse and the time series become more sinusoidal following the discussion earlier in this example.

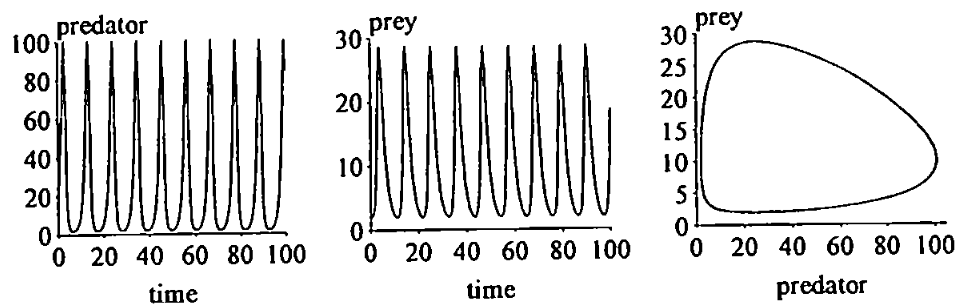


Figure 2.2: Solution curves for Equations 2.28 with $a_1 = 1$, $a_2 = 0.5$, $b_1 = 0.1$ and $b_2 = 0.02$ with a starting value of $(20, 2)$

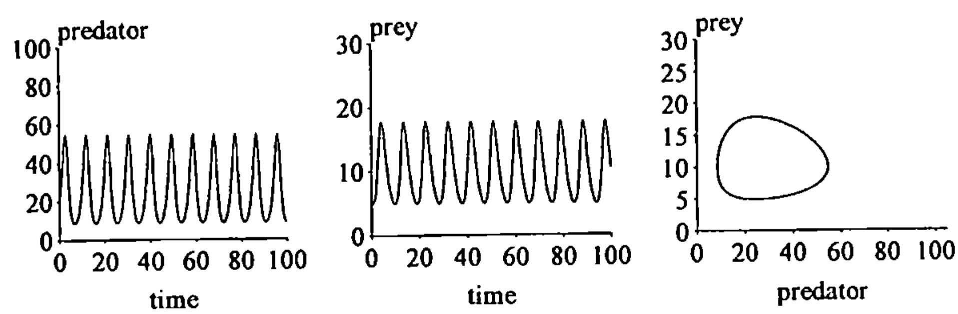


Figure 2.3: Solution curves for Equations 2.28 with $a_1 = 1$, $a_2 = 0.5$, $b_1 = 0.1$ and $b_2 = 0.02$ with a starting value of $(20, 5)$

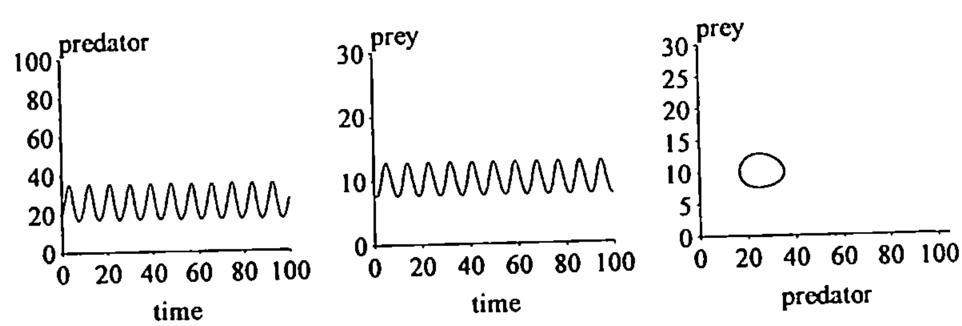


Figure 2.4: Solution curves for Equations 2.28 with $a_1 = 1$, $a_2 = 0.5$, $b_1 = 0.1$ and $b_2 = 0.02$ with a starting value of $(20, 8)$

Even though many textbooks, Edwards and Hamson, 1989, May,1973 and Pielou, 1977, for example, use this model as an example of stability analysis as Pielou, 1977, points out it is a totally unnatural model. The amplitudes of the oscillations are dependent only on the initial size of the populations and there is no effect of self limitation in either of the two populations. However it is a good example to demonstrate some of the mathematical techniques described earlier in this chapter.

### 2.4.2 Two Competing Species

Again this extremely simplified model can be used to illustrate some of the uses of stability analysis as well as including the self limiting factors which made the previous model so unrealistic. It is taken from Pielou, 1977. There are two species, $x$ and $y$, both competing for the same food source. The following simplifying assumptions are made about the two species.

- The food source is unlimited.
- Both species eat only this one source of food.
- The growth of each population is limited by the size of its own population and by the size of the competing population.

Therefore species $x$ will increase due to its consumption of the food source, will decrease due to the competition with $y$ and also decrease due to competition within its own population. The situation will be the same with species $y$. Hence the following set of differential equations could be used to model such a situation.

$$\frac{\mathrm{d}x}{\mathrm{d}t} = a_1 x - b_1 x^2 - c_1 xy, \tag{2.47a}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = a_2 y - b_2 y^2 - c_2 xy. \tag{2.47b}$$

Here the parameters can be described as follows: $a_1$ is the natural birth and death rate of $x$, $b_1$ is the competition effect for $x$ within its own species, $c_1$ is the competition effect on $x$ by $y$, $a_2$ is the natural birth and death rate of $y$, $b_2$ is the competition effect for $y$ by its own species and $c_2$ is the competition effect on $y$ by $x$.

In this situation the values of the parameters play a large part in the eventual outcome to the sizes of the two populations. The fixed points of the system occur when both sides of Equations 2.47 are equal to 0. One of the solutions is clearly $(0,0)$ which is when both species have died out. The other occurs when

$$a_1 - b_1x - c_1y = 0, \tag{2.48a}$$

$$a_2 - b_2y - c_2x = 0. \tag{2.48b}$$

which when solved give the fixed points as

$$x = \frac{a_1b_2 - a_2c_1}{b_1b_2 - c_1c_2} \tag{2.49}$$

$$y = \frac{a_2b_1 - a_1c_2}{b_1b_2 - c_1c_2} \tag{2.50}$$

Since the fixed point must be positive one can already see that there are certain constraints on the parameters from the beginning. However an analysis of the starting points can lead to some interesting conditions for which species survive.

From Equations 2.48 it can be seen that the locus of points for which $\frac{dx}{dt} = 0$ is on the line

$$x = \frac{a_1 - c_1y}{b_1} \tag{2.51}$$

which is known as the $x$-isocline and similarly the $y$-isocline is

$$y = \frac{a_2 - c_2x}{b_2}. \tag{2.52}$$

If at any time the population $x$ falls below the $x$-isocline i.e.

$$x < \frac{a_1 - c_1y}{b_1} \tag{2.53}$$

then

$$\begin{aligned}\frac{dx}{dt} &= x(a_1 - b_1 x - c_1 y) \\ &> x(a_1 - b_1(\frac{a_1 - c_1 y}{b_1}) - c_1 y) \\ &> 0\end{aligned} \tag{2.54}$$

and so species $x$ will increase. Conversely if the population $x$ is such that

$$x > \frac{a_1 - c_1 y}{b_1} \tag{2.55}$$

then $\frac{dx}{dt} < 0$ and so species $x$ will decrease. This can be illustrated graphically as in Figure 2.5(a). If the initial size of species $x$ lies in region 1 the size of the population will increase, if it lies in region 2 then its population size will decrease.

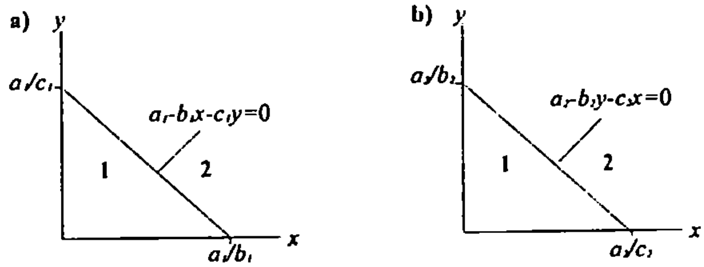


Figure 2.5: Initial population sizes for (a) species $x$ and (b) species y

A similar argument applies for species $y$; if the population size is such that $y < \frac{a_2 - c_2 x}{b_2}$ then the population will increase, If the population size is such that $y > \frac{a_2 - c_2 x}{b_2}$ the population will decrease as shown graphically in Figure 2.5(b).

By examining the two interacting populations it can therefore be discovered how they interact with each other and how the size of the population affects which species live or die. There are four possible relationships between the $x$-isocline and the $y$-isocline and therefore the parameter values and these are shown graphically in Figure 2.6.

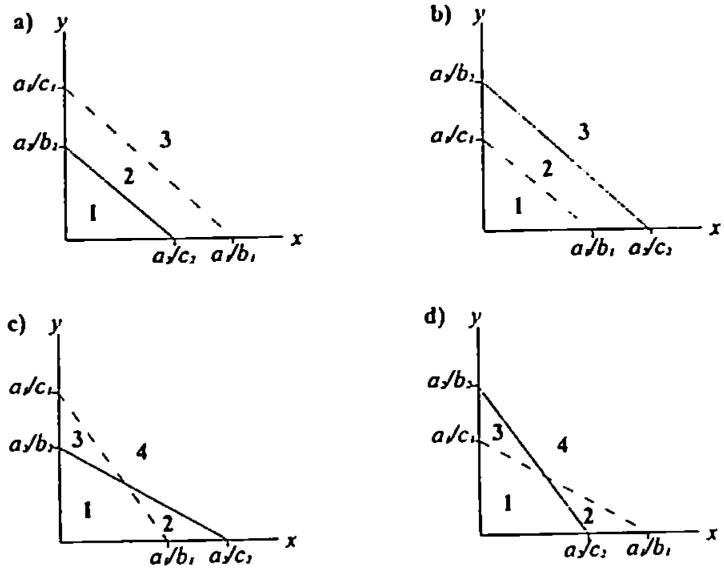


Figure 2.6: The four possible relationships between the isoclines $x = \frac{a_1 - c_1 y}{b_1}$ and $y = \frac{a_2 - c_2 x}{b_2}$

Let the combined population be such that

$$x < \frac{a_1 - c_1 y}{b_1} \tag{2.56}$$

and

$$y < \frac{a_2 - c_2 x}{b_2} \tag{2.57}$$

i.e. in region 1 of the graphs in Figure 2.6. There will be four possible outcomes to the two population sizes depending on the size of the parameter values with respect to each other. These outcomes respond to the four graphs a), b), c), and d) in Figure 2.6.

a) In this situation the two isoclines are such that $\frac{a_1}{c_1} > \frac{a_2}{b_2}$ and $\frac{a_1}{b_1} > \frac{a_2}{c_2}$ i.e. $a_1 b_2 > a_2 c_1$ and $a_1 c_2 > a_2 b_1$. It can be seen that in this case one of the fixed points will be positive and the other negative which implies that in this situation one of the two species will dominate forcing the other to die out. With both populations starting within region 1 they will increase. However as soon as the combined population is such that $y > \frac{a_2 - c_2 x}{b_2}$ i.e. in region 2 then species $y$ will decrease and species $x$ will take over causing species $y$ to die out.

b) This is the opposite situation to a) above in that now $\frac{a_2}{b_2} > \frac{a_1}{c_1}$ and $\frac{a_2}{c_2} > \frac{a_1}{b_1}$ i.e. $a_2 c_1 > a_1 b_2$ and $a_2 b_1 > a_1 c_2$. At first both populations will increase but when the combined population is within region 2 of Figure 2.6(b) then $\frac{dx}{dt} < 0$ and so eventually species $x$ will die out leaving $y$ to dominate.

c) In this case the conditions on the parameters are $\frac{a_1}{c_1} > \frac{a_2}{b_2}$ and $\frac{a_2}{c_2} > \frac{a_1}{b_1}$ i.e. $a_1b_2 > a_2c_1$ and $a_2b_1 > a_1c_2$. Looking at the fixed point, Equation 2.49, it can be seen that in this case for the fixed point to be positive then $b_1b_2 > c_1c_2$. The fixed point is where the two isoclines cross and the nature of this fixed point can be determined by analysing its stability. The Jacobian matrix for this system is

$$\mathbf{J} = \begin{bmatrix} a_1 - 2b_1x - c_1y & -c_1x \\ -c_2y & a_2 - 2b_2y - c_2x \end{bmatrix}_{\left(\frac{a_1b_2-a_2c_1}{b_1b_2-c_1c_2}, \frac{a_2c_1-a_1c_2}{b_1b_2-c_1c_2}\right)} \tag{2.58}$$

which since $a_1 - b_1x - c_1y = 0$ and $a_2 - b_2y - c_2x = 0$ at the fixed points simplifies very nicely to

$$\mathbf{J} = \begin{bmatrix} -b_1x & -c_1x \\ -c_2y & -b_2y \end{bmatrix}_{\left(\frac{a_1b_2-a_2c_1}{b_1b_2-c_1c_2}, \frac{a_2b_1-a_1c_2}{b_1b_2-c_1c_2}\right)} . \tag{2.59}$$

Let $(x_f, y_f)$ be the fixed point and therefore the resulting polynomial in $\lambda$ from $|\mathbf{J} - \lambda\mathbf{I})$ is

$$\lambda^2 + \lambda(b_1x_f + b_2y_f) + (b_1b_2 - c_1c_2)x_fy_f = 0. \tag{2.60}$$

Now by the Routh-Hurwitz criterion the system is stable if

$$i) \quad b_1x_f + b_2y_f > 0 \tag{2.61a}$$

$$ii) \quad (b_1b_2 - c_1c_2)x_fy_f > 0. \tag{2.61b}$$

In this case since the fixed points and $b_1b_2 > c_1c_2$, these two conditions are satisfied and so the fixed point in this case is a stable point. Therefore which ever region the combined population is in it will always gravitate towards the fixed point and so both populations will settle down and coexist together.

d) In this case the conditions on the parameters are $\frac{a_2}{b_2} > \frac{a_1}{c_1}$ and $\frac{a_1}{b_1} > \frac{a_2}{c_2}$ i.e. $a_2c_1 > a_1b_2$ and $a_1c_2 > a_2b_1$. For the fixed point to be positive then the condition $b_1b_2 < c_1c_2$ must be observed. Therefore this fixed point is not stable since Equation 2.61(b) is not satisfied and so the fixed point in this situation will be an unstable point and so the populations will diverge from that point. (The fixed point is not a centre either since that would require $\lambda$ to have zero real parts and this is not the case when solving Equation 2.60.) Ultimately one of the populations will die out leaving the other to dominate.

Figures 2.7 to 2.10 show each situation and the outcome given the starting population was in each region of the graphs in Figure 2.6.

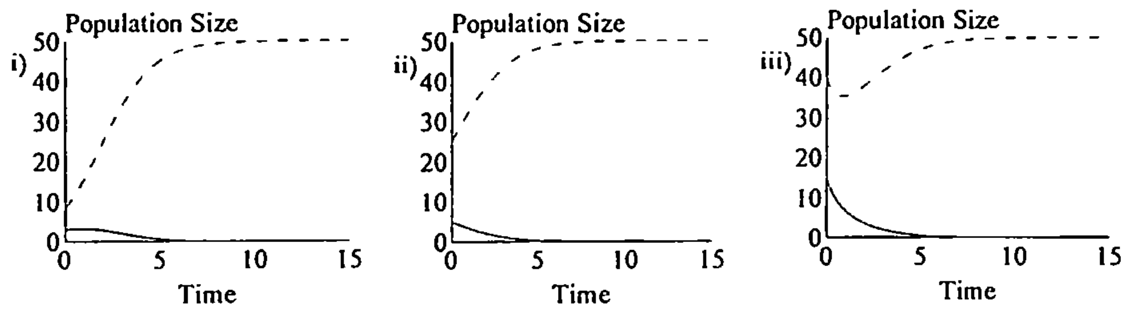


Figure 2.7: Solution curves of Equations 2.47 with $a_1 = 1.0$, $a_2 = 0.5$ $b_1 = 0.02$, $b_2 = 0.04$, $c_1 = 0.04$ and $c_2 = 0.025$ i.e. case (a) above with the starting point in i)Region 1, ii)Region 2 and iii) Region 3

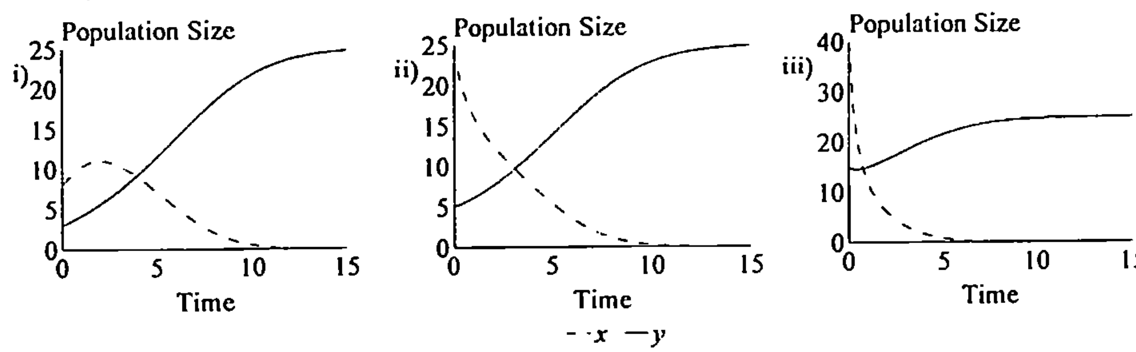


Figure 2.8: Solution curves of Equations 2.47 with $a_1 = 1.0$, $a_2 = 0.5$ $b_1 = 0.05$, $b_2 = 0.02$, $c_1 = 0.08$ and $c_2 = 0.01$ i.e. case (b) above with the starting point in i)Region 1, ii)Region 2 and iii) Region 3

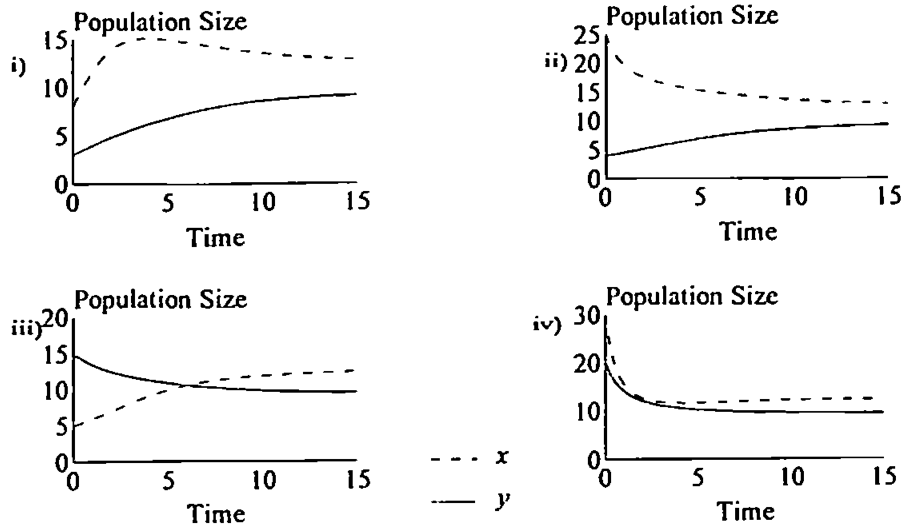


Figure 2.9: Solution curves of Equations 2.47 with $a_1 = 1.0$, $a_2 = 0.5$ $b_1 = 0.05$, $b_2 = 0.04$, $c_1 = 0.04$ and $c_2 = 0.01$ i.e. case (c) above with the starting point in i)Region 1, ii)Region, iii) Region 3 and iv) Region 4

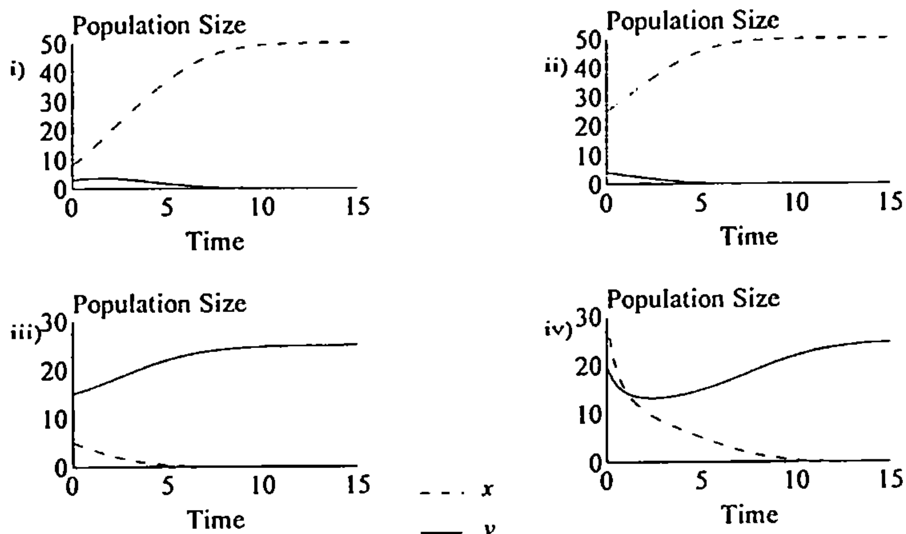


Figure 2.10: Solution curves of Equations 2.47 with $a_1 = 1.0$, $a_2 = 0.5$ $b_1 = 0.02$, $b_2 = 0.02$, $c_1 = 0.08$ and $c_2 = 0.025$ i.e. case (d) above with the starting point in i)Region 1, ii)Region 2, iii) Region 3 and iv) Region 4

This model shows how the parameters affect the outcome of the two populations. If one was trying to model such a competition situation then a time series plot of the data could be compared to the different plots above and the best match would produce the conditions on the parameters for that situation.

### 2.4.3 A Zooplankton, Phytoplankton and Nutrient model

This is a three variable model discussed by Klein and Steele, 1985. It models a simple nutrient cycle, $N$, through phytoplankton, $P$, and zooplankton, $Z$. The three differential equations are given by

$$\frac{\mathrm{d}Z}{\mathrm{d}t} = b_2PZ - dZ, \tag{2.62a}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = aNP - bPZ, \tag{2.62b}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -aNP + b_1PZ + d_1Z. \tag{2.62c}$$

The term $b_2PZ$ represents the growth of the zooplankton from eating the phytoplankton. The term $-dZ$ represents the natural deaths of the zooplankton. The term $aNP$ represents the growth of the phytoplankton by photosynthesis. The rate of photosynthesis (and therefore the rate of growth) depends on the available nutrients. The term $-bPZ$ represents the death of the phytoplankton from being eaten by the zooplankton. In the nutrient equation the term $-aNP$ represents the loss of nutrients from the surroundings which have been used by the phytoplankton for photosynthesis. The nutrients released into the surroundings when the phytoplankton get eaten by the zooplankton is represented by the term $b_1PZ$ and when the zooplankton die by $d_1Z$.

This model is an extremely simple one to represent what is a sophisticated procedure but it will enable some of the mathematical tools in Section 2.3 to be implemented. The authors have assumed a purely recycling model i.e. the ecosystem is completely enclosed. The amounts of phytoplankton, zooplankton and nutrients are all measured in the same units which are mg/m$^3$ i.e. the amount of nitrate per m$^3$. So let the total nitrate concentration be $N_0$. At any time $N+P+Z=N_0$ and so $\frac{\mathrm{d}(N+P+Z)}{\mathrm{d}t}=0$. For this to be true $b=b_1+b_2$ and $d=d_1$ in Equations 2.62.

One of the fixed points of Equations 2.62 is $(0,0,0)$ which is of no importance, the other occurs when

$$b_2P - d = 0, \tag{2.63a}$$

$$aN - bZ = 0, \tag{2.63b}$$

$$-aNP + b_1PZ + d_1Z \;=\; 0 \tag{2.63c}$$

which can be solved to give the fixed point $(Z_f, P_f, N_f)$

$$Z_f \;=\; \frac{N_0 - d/b_2}{1 + a/b}, \tag{2.64a}$$

$$P_f \;=\; \frac{d}{b_2}, \tag{2.64b}$$

$$N_f \;=\; \frac{N_0 - d/b_2}{1 + b/a}. \tag{2.64c}$$

The Jacobian matrix for this system is found to be

$$\mathbf{J} = \begin{bmatrix} 0 & b_2Z_f & 0 \\ -bP_f & 0 & aP_f \\ b_1P_f + d & \frac{-dZ_f}{P_f} & -aP_f \end{bmatrix}. \tag{2.65}$$

The polynomial in $\lambda$ resulting from $\det(\mathbf{J} - \lambda I)$ is

$$\lambda^3 + aP_f\lambda^2 + \lambda(daZ_f + bb_2Z_fP_f) + ab_2Z_fP_f(b_2P_f - d) = 0. \tag{2.66}$$

Now $P_f = d/b_2$ and so $b_2P_f - d = 0$ and so

$$\lambda^2 + aP_f\lambda + Z_f(ad + bb_2P_f) = 0. \tag{2.67}$$

So the three variable model is in effect only a two variable model. This comes about because of the condition $Z + P + N = N_0$ where $N_0$ is a constant. Any closed three variable model can therefore be regarded as a two variable system.

If the system was a stable one then the constraints on the parameters would be

$$i) \quad aP_f > 0, \tag{2.68a}$$

$$ii) \quad Z_f(ad + bb_2P_f) > 0. \tag{2.68b}$$

Now since all parameters and all fixed points are positive then these two conditions are automatically satisfied and the system is always stable. So after some length of time the three variables will settle down to their fixed points as shown in Figure 2.11.

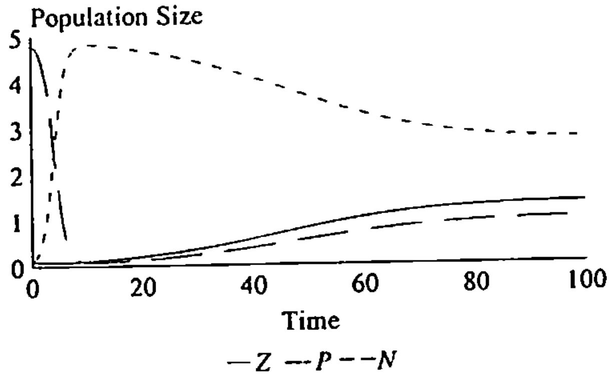


Figure 2.11: Solution curves for Equations 2.62 with $a = 0.2$, $b = 0.15$, $b_1 = 0.12$, $b_2 = 0.03$ and $d = 0.08$. The initial conditions are $N = 4.8$, $P = 0.1$ and $Z = 0.1$ i.e. $N_0 = 5$

Although this model does not accurately model a phytoplankton, zooplankton and nutrient system it has been useful in demonstrating that by imposing some conditions the number of variables can be reduced. This is also bought into effect in the following two chapters (3 and 4) when a geometrical approach is examined.

## 2.5 Summary

This chapter has been an introduction to some of the techniques which are employed in the formulation and analysis of the models which are to follow. The basic building blocks of the modelling process have been discussed; the assumptions and simplifications, the translation into mathematics. Some mathematical (and statistical) tools have been examined which are necessary to aid the formulation of the model and to analyse how it behaves. These included stability analysis and how to deal with data. The chapter concluded with three examples of models which put into practice some of the mathematics discussed. This chapter is a preparation for the model building process in the next two chapters where a slightly different approach to the modelling of interacting populations is established.

# Chapter 3

# A Geometrical Approach

## 3.1 Introduction

In the previous chapter the classical technique of modelling populations was examined. In the next two chapters a new procedure is presented which removes some of the ambiguities that usually face the modeller. The method involves starting with solutions and working backwards to achieve the differential equations which form the basis of the model.

Any three variable model can be visualised by considering a three-dimensional shape. For any one point on the surface its coordinates $(x_1, x_2, x_3)$ can be obtained and so a value for $x_1$, $x_2$ and $x_3$ can be found. A curve can be represented by three parametric equations, $x_1 = f_1(t)$, $x_2 = f_2(t)$ and $x_3 = f_3(t)$ where $t$ is time. As time progresses the curve is traced out, each point on the curve corresponding to allowable values of $x_1$, $x_2$ and $x_3$. If, in addition, $f(x_1, x_2, x_3) = 0$ this means that the curve is embedded in a three-dimensional surface (given by $f(x_1, x_2, x_3) = 0$). The three-dimensional surface corresponds to a *constraint* on the variables $x_1$, $x_2$, and $x_3$ similar to that discussed in Klein and Steele's model in Section 2.4 in the previous chapter where the surface was a plane. A time dependent model can be formulated by differentiating $x_1(t)$, $x_2(t)$ and $x_3(t)$ with respect to time $t$. It is this kind of model that will be considered here. If the curve on the surface moves in such a way that simulates population changes within an ecosystem then the model has been constructed successfully. In order for the models to be used, very little needs be known about the populations in terms of their biology, only how the population sizes vary with time. Once the equations have been formulated then the modeller can examine them and observe which variables are interacting to cause the path to behave as it does; these types of models can therefore be described as learning models. From them one can ascertain how each individual species might interact to form large multi-species ecosystems.

Once the method has been established in three–dimensions one can then proceed to widen the scope of the models by moving into higher dimensions using the same principle. Two shapes are examined; an ellipsoid and a torus. The higher dimensional 'shapes' follow the same basic formulation as the three–dimensional ones, only it is impossible to be able to visualize the solution curves. This visualisation is one of the most useful novel aspects of the three dimensional approach.

## 3.2 An Ellipsoid

### 3.2.1 Formulating the Model

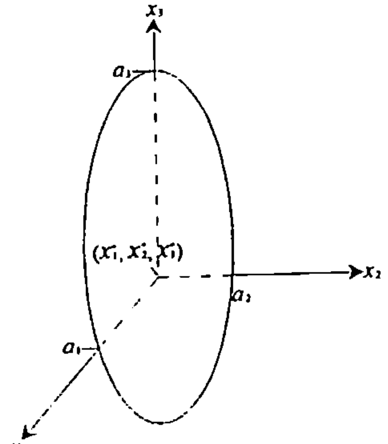


Figure 3.1: Ellipsoid, centred at $(x_1^*, x_2^*, x_3^*)$ with characteristic parameters $a_1$, $a_2$ and $a_3$

The ellipsoid is one of the simplest geometrical shapes. Its characteristic equation is easily parameterized and so is an ideal choice to illustrate the principle of geometric modelling.

The equation of the ellipsoid in Figure 3.1 is given by

$$\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2} = 1 \tag{3.1}$$

where $x_1^* > a_1$, $x_2^* > a_2$ and $x_3^* > a_3$ to ensure that the ellipsoid is entirely within the positive quadrant.

This equation can be parameterized using the spherical polar coordinate system $r$, $\theta_1$ and $\theta_2$ as shown in Figure 3.2.

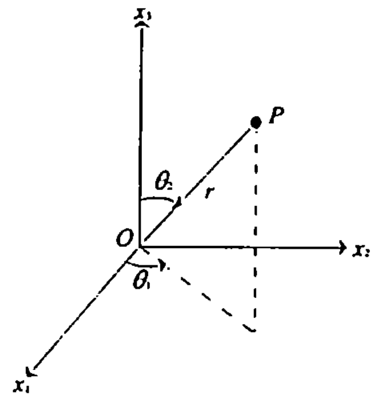


Figure 3.2: Spherical polar coordinates

$P$ is a point on the surface of the sphere with rectangular cartesian coordinates $(x_1, x_2, x_3)$. $r$ is the distance of $P$ from the origin $O$, $\theta_1$ is the angle between the $x_1x_2$ plane and the plane containing $P$ and the $x_3$ axis and $\theta_2$ is the angle that $OP$ makes with the $x_3$ axis. The angles are measured positive in the senses shown in Figure 3.2. Hence $r$, $\theta_1$ and $\theta_2$ are the spherical polar coordinates of $P$. Therefore $x_1$, $x_2$ and $x_3$ can be related to the spherical coordinates by $x_1 = r\sin\theta_2\cos\theta_1$, $x_2 = r\sin\theta_2\sin\theta_1$ and $x_3 = r\cos\theta_2$. The ellipsoid can be parameterized as follows:

$$x_1 - x_1^* = a_1 \sin\theta_2 \cos\theta_1 \tag{3.2a}$$

$$x_2 - x_2^* = a_2 \sin\theta_2 \sin\theta_1 \tag{3.2b}$$

$$x_3 - x_3^* = a_3 \cos\theta_2. \tag{3.2c}$$

with $r$ being replaced by $a_1$, $a_2$ or $a_3$ to take account of the nonspherical shape of the ellipsoid.

Keeping the system as general as possible by letting

$$\theta_1 = \alpha_1 f_1(t) + \phi_1 \tag{3.3a}$$

$$\theta_2 = \alpha_2 f_2(t) + \phi_2 \tag{3.3b}$$

a set of parametric equations for Equation 3.1 is as follows:

$$x_1 - x_1^* = a_1 \sin(\alpha_2 f_2(t) + \phi_2)\cos(\alpha_1 f_1(t) + \phi_1) \tag{3.4a}$$

$$x_2 - x_2^* = a_2 \sin(\alpha_2 f_2(t) + \phi_2)\sin(\alpha_1 f_1(t) + \phi_1) \tag{3.4b}$$

$$x_3 - x_3^* = a_3 \cos(\alpha_2 f_2(t) + \phi_2) \tag{3.4c}$$

where $\alpha_1$, $\alpha_2$, $\phi_1$ and $\phi_2$ are parameters and $f_1(t)$ and $f_2(t)$ are functions of time $t$.

Differentiating Equations 3.4 with respect to time, the following set is obtained.

$$\begin{aligned}\frac{\mathrm{d}x_1}{\mathrm{d}t} &= a_1\alpha_2 f_2'(t)\cos(\alpha_1 f_1(t) + \phi_1)\cos(\alpha_2 f_2(t) + \phi_2) \\ &\quad -a_1\alpha_1 f_1'(t)\sin(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_2 f_2(t) + \phi_2)\end{aligned} \tag{3.5a}$$

$$\begin{aligned}\frac{\mathrm{d}x_2}{\mathrm{d}t} &= a_2\alpha_2 f_2'(t)\sin(\alpha_1 f_1(t) + \phi_1)\cos(\alpha_2 f_2(t) + \phi_2) \\ &\quad +a_2\alpha_1 f_1'(t)\cos(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_2 f_2(t) + \phi_2)\end{aligned} \tag{3.5b}$$

$$\frac{\mathrm{d}x_3}{\mathrm{d}t} = -a_3\alpha_2 f_2'(t)\sin(\alpha_2 f_2(t) + \phi_2) \tag{3.5c}$$

where $f'(t)$ denotes the derivative with respect to time of the function $f(t)$. Using Equations 3.1 3.4 and the identity $\sin^2\Theta + \cos^2\Theta = 1$, $\sin(\alpha_1 f_1(t) + \phi_1)$, $\cos(\alpha_1 f_1(t) + \phi_1)$ etc. can be expressed in terms of $x_1$, $x_2$ and $x_3$ as follows:-

$$\sin(\alpha_2 f_2(t) + \phi_2) = \sqrt{\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}} \tag{3.6a}$$

$$\cos(\alpha_2 f_2(t) + \phi_2) = \frac{x_3 - x_3^*}{a_3} \tag{3.6b}$$

$$\sin(\alpha_1 f_1(t) + \phi_1) = \frac{x_2 - x_2^*}{a_2\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2}}} \tag{3.6c}$$

$$\cos(\alpha_1 f_1(t) + \phi_1) = \frac{x_1 - x_1^*}{a_1\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2}}} \tag{3.6d}$$

and therefore Equations 3.5 can be written

$$\frac{dx_1}{dt} = \frac{\alpha_2 f_2'(t)(x_1 - x_1^*)(x_3 - x_3^*)}{a_3\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2}}} - \frac{a_1\alpha_1}{a_2} f_1'(t)(x_2 - x_2^*) \tag{3.7a}$$

$$\frac{dx_2}{dt} = \frac{\alpha_2 f_2'(t)(x_2 - x_2^*)(x_3 - x_3^*)}{a_3\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2}}} + \frac{a_2\alpha_1}{a_1} f_1'(t)(x_1 - x_1^*) \tag{3.7b}$$

$$\frac{dx_3}{dt} = -a_3\alpha_2 f_2'(t)\sqrt{\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}} \tag{3.7c}$$

Equations 3.7 therefore model a three variable system whose solution curves 'wander' over the surface of the ellipsoid

$$\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2} = 1 \tag{3.8}$$

Even though these equations do not appear to exhibit a form appropriate to any well known three variable ecosystem model they do form a *basis* for such a model. The functions $f_1(t)$ and $f_2(t)$ can be any differentiable functions of $t$ whatsoever and the solution curve will still lie on the ellipsoid. Such functions will be in terms of $x_1$, $x_2$ and $x_3$ so that when substituted into Equations 3.7 above they will add further terms to the model. Appropriate choices of $f_1(t)$ and $f_2(t)$ can be chosen to fit the model to different situations. First, however, by examining the mathematics of the system in a little more depth it can be determined exactly how the path behaves.

By considering the system in the spherical coordinates, $\theta_1$ and $\theta_2$, it will be easier to see the path's behaviour. As mentioned before, $\theta_1$ is the angle between the $x_1x_2$ plane and the plane containing a point on the surface and the $x_3$ axis. Therefore if $\theta_1$ is monotonically increasing then this implies that the path travels in an anticlockwise direction around the ellipsoid. From Equation 3.3a it can be seen that $\theta_1$ is a function of $f_1(t)$. Therefore the choice of $f_1'(t)$ (and so $f_1(t)$) that is made in simplifying the equations will determine whether or not the path circles around the ellipsoid. If $f_1(t)$ increases with time $t$ then $\theta_1$ also increases, and so the solution curve will continue to travel around the ellipsoid. If on the other hand a situation led to the solutions having constant $x_1$ or $x_2$ (i.e. the path ceases to circle the ellipsoid) a choice of $f_1(t)$ could be made so that this occurred. Already one can see the power of this approach. From the one basic model a multitude of different situations can be modelled.

However it is still not known if the path continues to travel down the ellipsoid as it winds itself round or if it stops at any point (i.e. with constant $x_3$.) By considering how $x_3$ behaves as time $t$ increases will answer this problem. From Equations 3.4 it can be seen that $x_3$ is a function of $f_2(t)$. So it is the choice of $f_2(t)$ which will determine if the path moves up or down the ellipsoid in the $x_3$ direction or if it stops at any point. Analysis of the fixed points of the system will also give some indication of the nature of the path on the surface.

### 3.2.2 Many Models From One

In this section various choices will be made for $f_1(t)$ and $f_2(t)$ to examine how they cause the solutions to behave and what types of situations each model may be able to simulate.

This work is devoted to analytical solutions, avoiding the use of complex numerical methods and to introduce the concept of such a modelling procedure. It is therefore essential to keep the model as simple as possible. When considering choices for $f_2'(t)$ it seems an ideal opportunity to deal with the square root term which appears in all three of Equations

3.7. Therefore a sensible choice is to let

$$f_2'(t) = f_3(t)\sqrt{\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}} \tag{3.9}$$

where $f_3(t)$ is a function of time $t$ which can be chosen at a later stage. Therefore the general model in this case is

$$\frac{dx_1}{dt} = \frac{\alpha_2 f_3(t)}{a_3}(x_1 - x_1^*)(x_3 - x_3^*) - \frac{a_1\alpha_1 f_1'(t)}{a_2}(x_2 - x_2^*) \tag{3.10a}$$

$$\frac{dx_2}{dt} = \frac{\alpha_2 f_3(t)}{a_3}(x_2 - x_2^*)(x_3 - x_3^*) + \frac{a_2\alpha_1 f_1'(t)}{a_1}(x_1 - x_1^*) \tag{3.10b}$$

$$\frac{dx_3}{dt} = -a_3\alpha_2 f_3(t)(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}) \tag{3.10c}$$

#### 3.2.2.1 Model 1

For this first model the choices for the two functions $f_1(t)$ and $f_3(t)$ are those that make it the simplest possible. Choices of

$$f_1'(t) = 1 \tag{3.11}$$

$$f_3(t) = 1 \tag{3.12}$$

produce the following set of differential equations.

$$\frac{dx_1}{dt} = \frac{\alpha_2}{a_3}(x_1 - x_1^*)(x_3 - x_3^*) - \frac{a_1\alpha_1}{a_2}(x_2 - x_2^*) \tag{3.13a}$$

$$\frac{dx_2}{dt} = \frac{\alpha_2}{a_3}(x_2 - x_2^*)(x_3 - x_3^*) + \frac{a_2\alpha_1}{a_1}(x_1 - x_1^*) \tag{3.13b}$$

$$\frac{dx_3}{dt} = -a_3\alpha_2(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}) \tag{3.13c}$$

Looking first at $f_1(t)$ will give an indication of how the path travels around the ellipsoid. Therefore integrating 3.11 gives

$$f_1(t) = t + k_1 \tag{3.14}$$

where $k_1$ is the constant of integration. Consequently Equation 3.3a becomes

$$\theta_1 = \alpha_1(t + k_1) + \phi_1 \tag{3.15}$$

So, for this simple model, as time $t$ increases, the angle $\theta_1$ also increases and the solution curve winds itself around the ellipsoid.

Examination of the fixed points of this system may give an indication to whether the path moves up or down the ellipsoid as it winds itself around. The fixed points of the model governed by Equations 3.13 occur when

$$\begin{aligned}
\frac{\alpha_2}{a_3}(x_1 - x_1^*)(x_3 - x_3^*) - \frac{a_1\alpha_1}{a_2}(x_2 - x_2^*) &= 0 && (3.16a)\\
\frac{\alpha_2}{a_3}(x_2 - x_2^*)(x_3 - x_3^*) - \frac{a_2\alpha_1}{a_1}(x_1 - x_1^*) &= 0 && (3.16b)\\
-a_3\alpha_2\left(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}\right) &= 0 && (3.16c)
\end{aligned}$$

Equation 3.16c is satisfied when $\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2} = 0$. However it can be seen from Equation 3.8 that $\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2} = 1 - \frac{(x_3-x_3^*)^2}{a_3^2}$ and so Equation 3.16c can be solved to give

$$x_3 = x_3^* \pm a_3 \tag{3.17}$$

By substituting $x_3 = x_3^* - a_3$ into Equations 3.16a and 3.16b they can be solved to give the fixed point $x_1 = x_1^*$, $x_2 = x_2^*$ and $x_3 = x_3^* - a_3$ which is the bottom point of the ellipsoid. Similarly substituting $x_3 = x_3^* + a_3$ into Equations 3.16 produces the second fixed point $x_1 = x_1^*$, $x_2 = x_2^*$ and $x_3 = x_3^* + a_3$ which is the top point of the ellipsoid. Therefore this system of equations has two fixed points and determining whether they are stable or unstable will give an indication as to whether the path moves up or down the ellipsoid.

To investigate the stability of the fixed points the Jacobian matrix for Equations 3.13 and its associated eigenvalues need to be found as described in Section 2.3.2 in the previous chapter. The Jacobian matrix is found to be

$$J = \begin{bmatrix} \frac{\alpha_2(x_3-x_3^*)}{a_3} & -\frac{a_1\alpha_1}{a_2} & \frac{\alpha_2(x_1-x_1^*)}{a_3} \\ \frac{a_2\alpha_1}{a_1} & \frac{\alpha_2(x_3-x_3^*)}{a_3} & \frac{\alpha_2(x_2-x_2^*)}{a_3} \\ \frac{-2a_3\alpha_2(x_1-x_1^*)}{a_1^2} & \frac{-2a_3\alpha_2(x_2-x_2^*)}{a_2^2} & 0 \end{bmatrix} \tag{3.18}$$

which when evaluated at the fixed point $x_1 = x_1^*$, $x_2 = x_2^*$, $x_3 = x_3^* + a_3$ produces the extremely simple matrix

$$J = \begin{bmatrix} \alpha_2 & -\frac{a_1\alpha_1}{a_2} \\ \frac{a_2\alpha_1}{a_1} & \alpha_2 \end{bmatrix} \tag{3.19}$$

Solving $|J - \lambda I|$ produces the eigenvalues $\lambda = \alpha_2 \pm i\alpha_1$ and therefore the fixed point $(x_1^*, x_2^*, x_3^* + a_3)$ is an unstable fixed point since the real part of each eigenvalue is positive.

Similarly using the same procedure with the other fixed point, $(x_1^*, x_2^*, x_3^* - a_3)$ the eigenvalues are $\lambda = -\alpha_2 \pm i\alpha_1$ and therefore this fixed point is a stable point since the eigenvalues have negative real parts.

Therefore the path will tend to travel away from the top of the ellipsoid towards the bottom and when it reaches the bottom it will stay there. So, the path traced out by the

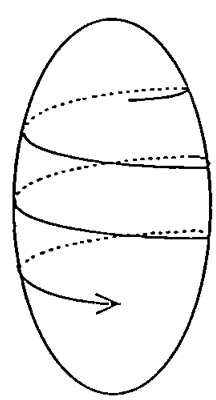

Figure 3.3: A typical solution curve of Equations 3.13 on the surface of the ellipsoid

solution will wind its way around and down the ellipsoid as shown in Figure 3.3.

Equations 3.13 can be interpreted in terms of an ecosystem consisting of three species $x_1$, $x_2$ and $x_3$.

- $x_1$ grows from the presence of $x_3$ and dies from the presence of $x_2$.
- $x_2$ grows from the presence of $x_1$ and $x_3$.
- $x_3$ dies from the presence of $x_1$ and $x_2$.

Therefore the model described by Equations 3.13 may be applied to a three variable ecosystem consisting of a herbivore, $x_1$, an omnivore, $x_2$, and a plant source, $x_3$. At the beginning of the period being modelled the plant source is plentiful but it is being consumed at a faster rate than which it regenerates. The herbivore and the omnivore are competing for the plant source but the omnivore has the advantage of having the alternative food source in the herbivore. The fluctuations within the herbivore and omnivore population sizes are due to the cyclic nature of such ecosystems. At the beginning of the period of study there is a certain amount of each in the area being studied. The omnivore is eating the herbivore until the herbivore population begins to decrease. Now there are less herbivores around for the omnivore to eat and so that population will start to decrease. Now, with less predation the herbivore population can start to increase again. However this in turn leads to the omnivore population increasing; there is more for them to eat and the cycle begins again. However the controlling factor in this ecosystem is the plant source. When the plant source reaches a certain level though it remains at that level. This occurs when all three populations are interacting with each other so that there is no change in the population size; they are dying and regenerating at the same rate. A steady state has therefore been reached.

The two parameters $\alpha_1$ and $\alpha_2$ govern how the solution curve travels down the ellipsoid. $\alpha_2$ is proportional to the rate at which $x_1$ and $x_2$ deplete $x_3$. Therefore the larger the value of $\alpha_2$ the faster $x_3$ will be depleted and the faster the solution curve will reach the bottom of the ellipsoid. $\alpha_1$ is proportional to the rate at which $x_1$ and $x_2$ interact with each other.

In terms of the solution curve this parameter therefore governs the number of coils around the ellipsoid. The larger the value of $\alpha_1$ the more times the solution curve coils around the ellipsoid on the way down.

Time series plots for different values of $\alpha_1$ and $\alpha_2$ are shown in Figures 3.4 to 3.6. Apart from varying $\alpha_1$ and $\alpha_2$ to produce different situations the 'shape' of the ellipsoid can be varied to give different types of solution curves. In Figures 3.7 to 3.9 the parameters $a_1$, $a_2$ and $a_3$ have been changed to produce differently 'shaped' ellipsoids.

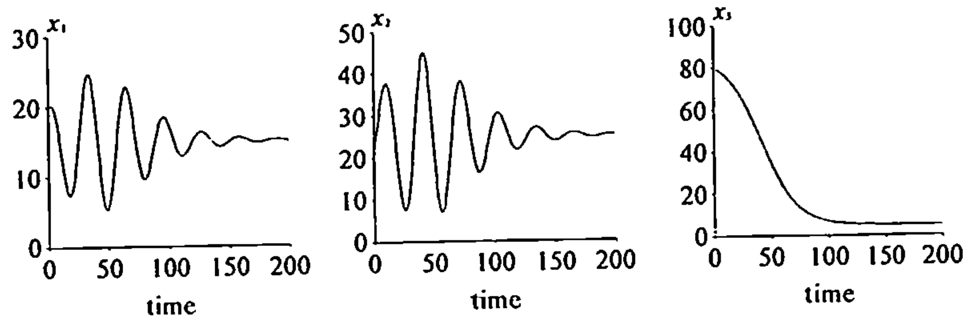


Figure 3.4: Solution curves of Equations 3.13 with $a_1$=10, $a_2$=20, $a_3$=40, $(x_1^*, x_2^*, x_3^*)$ = (15, 25, 45), $\alpha_1 = 0.2$, $\alpha_2 = 0.032$

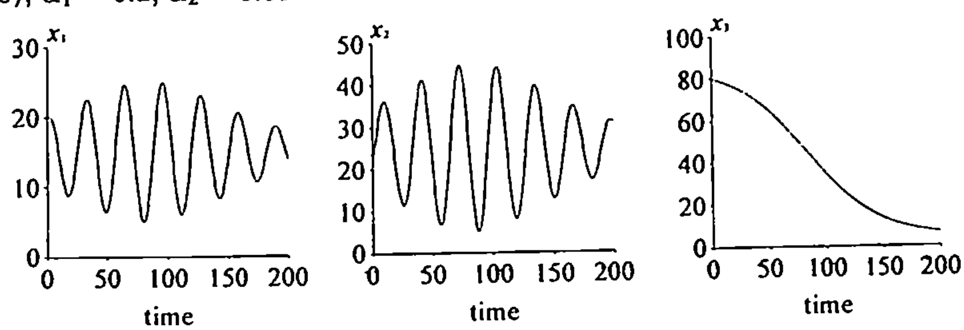


Figure 3.5: Solution curves of Equations 3.13 with $a_1$=10, $a_2$=20, $a_3$=40, $(x_1^*, x_2^*, x_3^*)$ = (15, 25, 45), $\alpha_1 = 0.2$, $\alpha_2 = 0.016$

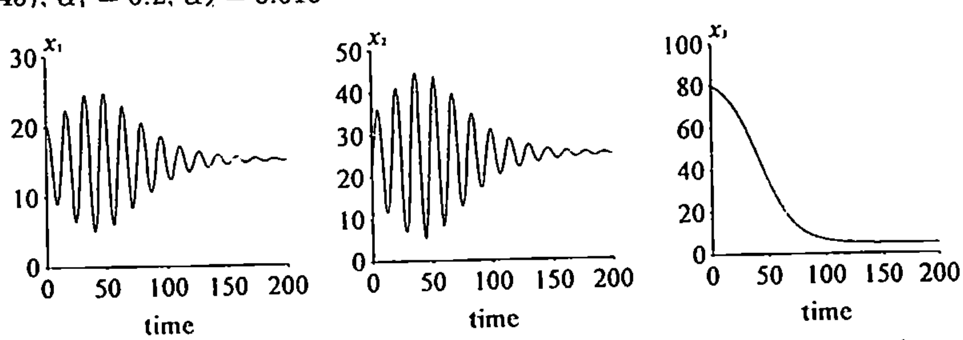


Figure 3.6: Solution curves of Equations 3.13 with $a_1$=10, $a_2$=20, $a_3$=40, $(x_1^*, x_2^*, x_3^*)$ = (15, 25, 45), $\alpha_1 = 0.4$, $\alpha_2 = 0.032$

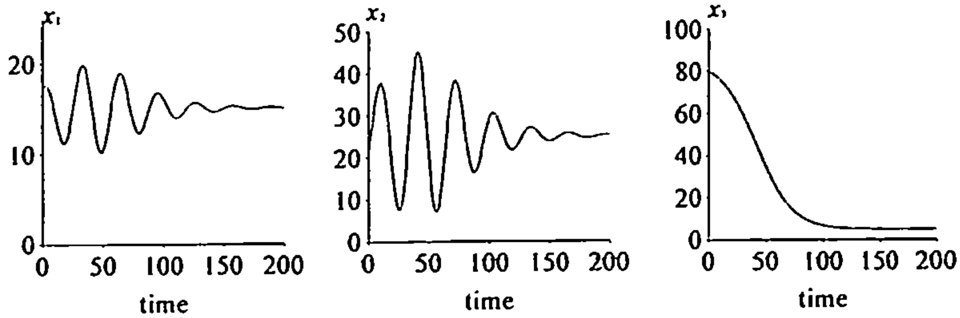


Figure 3.7: Solution curves of Equations 3.13 with $a_1$=5, $a_2$=20, $a_3$=40, $(x_1^*, x_2^*, x_3^*)$ = (15,25,45), $\alpha_1 = 0.2$, $\alpha_2 = 0.032$

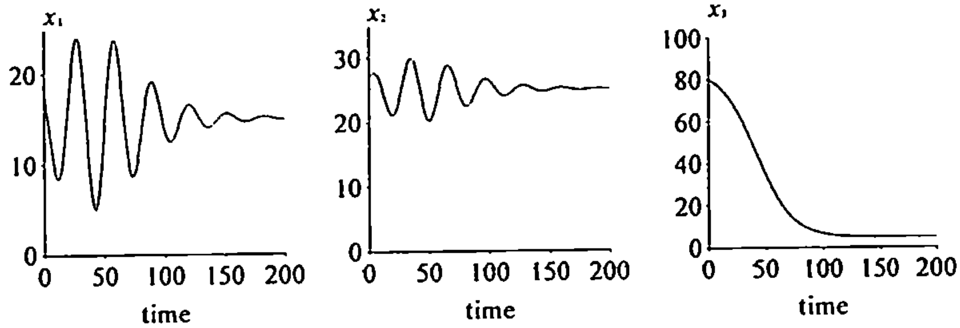


Figure 3.8: Solution curves of Equations 3.13 with $a_1$=10, $a_2$=5, $a_3$=40, $(x_1^*, x_2^*, x_3^*)$ = (15,25,45), $\alpha_1 = 0.2$, $\alpha_2 = 0.032$

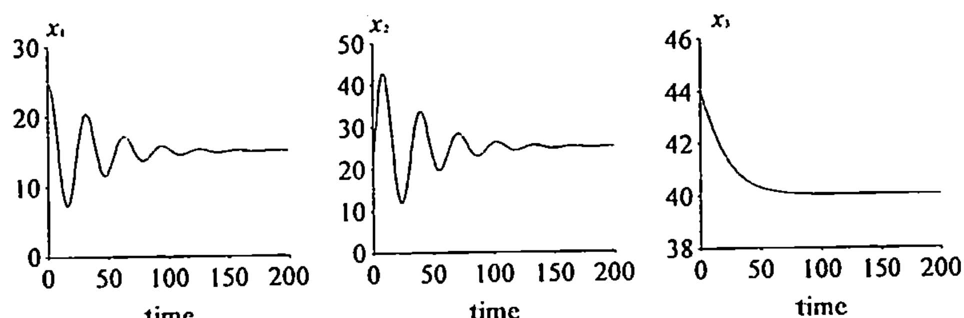


Figure 3.9: Solution curves of Equations 3.13 with $a_1$=10, $a_2$=20, $a_3$=5, $(x_1^*, x_2^*, x_3^*)$ = (15,25,45), $\alpha_1 = 0.2$, $\alpha_2 = 0.032$

#### 3.2.2.2 Model 2

Many typical modellers argue that if the second terms on the right hand side of Equations 3.7 (a) and (b) are to represent the effect of $x_1$ on $x_2$ and vice versa it should include an $x_1x_2$ term. The versatility of the general model (Equations 3.10) can be utilised to facilitate this. For example choices of

$$f_1'(t) = (x_1 - x_1^*)(x_2 - x_2^*) \tag{3.20}$$

$$f_3(t) = 1 \tag{3.21}$$

in these equations produce the following set of differential equations.

$$\frac{dx_1}{dt} = \frac{\alpha_2}{a_3}(x_1 - x_1^*)(x_3 - x_3^*) - \frac{a_1\alpha_1}{a_2}(x_2 - x_2^*)^2(x_1 - x_1^*) \tag{3.22a}$$

$$\frac{dx_2}{dt} = \frac{\alpha_2}{a_3}(x_2 - x_2^*)(x_3 - x_3^*) + \frac{a_2\alpha_1}{a_1}(x_1 - x_1^*)^2(x_2 - x_2^*) \tag{3.22b}$$

$$\frac{dx_3}{dt} = -a_3\alpha_2(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}) \tag{3.22c}$$

In this model to ascertain the path of the solution curve around the ellipsoid examination of $f_1(t)$ is needed. Equation 3.20 can be expressed as

$$\frac{df_1}{dt} = a_1 a_2 \sin^2(\alpha_2 f_2(t) + \phi_2)\cos(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_1 f_1(t) + \phi_1) \tag{3.23}$$

and so

$$\int \frac{df_1}{\cos(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_1 f_1(t) + \phi_1)} = \int a_1 a_2 \sin^2(\alpha_2 f_2(t) + \phi_2)dt \tag{3.24}$$

The above equation can be integrated to give

$$\alpha_1 f_1(t) + \phi_1 = \tan^{-1}[2\exp(\frac{-2\alpha_1 a_1 a_2}{\alpha_2 \exp(2\alpha_2(t + k_2) + 1)})] \tag{3.25}$$

where $k_2$ is the constant of integration. The details of this integration are given in Appendix A.

Hence for this model Equation 3.3a becomes

$$\theta_1 = \tan^{-1}[2\exp(\frac{-2\alpha_1 a_1 a_2}{\alpha_2 \exp(2\alpha_2(t + k_2) + 1)})] \tag{3.26}$$

Now the maximum value of $\tan^{-1}(x)$ is $\pi/2$ and since $\exp(\frac{-2\alpha_1 a_1 a_2}{\alpha_2 e^{2\alpha_2(t+k_2)+1)}})$ is always greater than 0, $\theta_1$ lies in the range $0 \leq \theta_1 \leq \pi/2$. Now $\theta_1$ is the angle between the $x_1 x_2$

plane and the plane containing a point on the surface and the $x_3$ axis. Therefore the path will never travel further than 90° from the $x_1$ axis. This can be seen by looking at $\frac{d\theta_1}{dt}$.

$$\frac{d\theta_1}{dt} = \alpha_1 f_1'(t) \tag{3.27}$$

$$= \alpha_1(x_1 - x_1^*)(x_2 - x_2^*) \tag{3.28}$$

From this it can be seen that whenever either $x_1 = x_1^*$ or $x_2 = x_2^*$ then $\frac{d\theta_1}{dt} = 0$, $\theta_1$ stops increasing and so the path will cease circling the ellipsoid. From Equation 3.28, if the starting point is such that $x_1 > x_1^*$ and $x_2 > x_2^*$ or $x_1 < x_1^*$ and $x_2 < x_2^*$ then $\frac{d\theta_1}{dt} > 0$ and therefore $\theta_1$ will increase and travel in an anticlockwise direction around the ellipsoid until it reaches the plane $x_1 = x_1^*$ and the path will cease circling. If the starting point is such that $x_1 > x_1^*$ and $x_2 < x_2^*$ or $x_1 < x_1^*$ and $x_2 > x_2^*$ then $\frac{d\theta_1}{dt} < 0$ and therefore $\theta_1$ will decrease and travel in an clockwise direction around the ellipsoid until it reaches the plane $x_1 = x_1^*$ and the path will cease circling. The movement of the path around the ellipsoid will thus solely depend on the starting point. Considering an $xy$ plane view of the ellipsoid as shown in Figure 3.10, the starting point can be in any of the four quadrants bounded by the lines $\frac{x_1^2}{a_1^2} + \frac{x_2^2}{a_2^2} = 1$, $x_1 = x_1^*$ and $x_2 = x_2^*$.

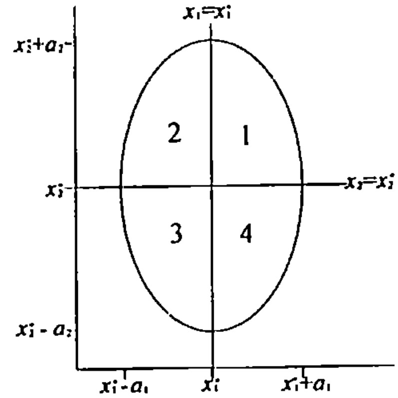


Figure 3.10: $xy$ plane view of the ellipsoid at $x_3 = x_3^*$

Therefore if the starting point is in quadrants 1 or 3 then the path will move in an anticlockwise direction towards the line $x_1 = x_1^*$. If the starting point is in quadrants 2 or 4 then the path will move in a clockwise direction towards the line $x_1 = x_1^*$.

Carrying out the stability analysis for this model the fixed points are once more found to be $(x_1^*, x_2^*, x_3^* + a_3)$ and $(x_1^*, x_2^*, x_3^* - a_3)$. At the fixed point $(x_1^*, x_2^*, x_3^* + a_3)$ the Jacobian matrix is simply

$$J = \begin{bmatrix} \alpha_2 & 0 \\ 0 & \alpha_2 \end{bmatrix} \tag{3.29}$$

Solving $|J - \lambda I|$ produces the repeated eigenvalues $\lambda = \alpha_2$ and therefore the fixed point is an unstable point. Similarly with the point $(x_1^*, x_2^*, x_3^* - a_3)$ the repeated eigenvalues are $\lambda = -\alpha_2$ and so this point is a stable fixed point.

Therefore the path will continue to move *down* the ellipsoid when $x_1$ reaches $x_1^*$ and a typical solution curve on the surface is shown in Figure 3.11.

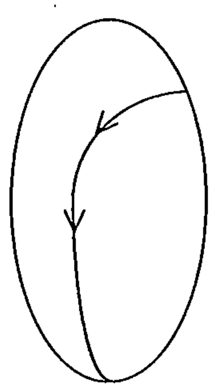

Figure 3.11: A typical solution curve of Equations 3.22 on the surface of the ellipsoid

Equations 3.22 can again be interpreted in terms of an ecosystem consisting of three species $x_1$, $x_2$ and $x_3$.

- $x_1$ grows from the presence of $x_3$ and dies from the presence of $x_2$.
- $x_2$ grows from the presence of $x_1$ and $x_3$.
- $x_3$ dies from the presence of $x_1$ and $x_2$.

Therefore the model described by Equations 3.22 may again be applied to a three variable ecosystem consisting of a herbivore, $x_1$, an omnivore, $x_2$, and a plant source, $x_3$. However, this model produces a situation where once the herbivore, $x_1$, has reached a certain level, $x_1^*$, its natural growth rate is matched by its death rate. The fluctuations produced in

Model 1 do not occur and all three populations quickly settle down to exist together in equilibrium. This is a similar concept to the 'carrying capacity' of such models as those for competition as discussed in Section 2.4.2 and the phytoplankton, zooplankton and nitrate model of Klein and Steele discussed in Section 2.4.3.

Figures 3.12 to 3.15 show solution curves for equations 3.22 for four different starting points around the ellipsoid. In each case it can be seen that the path moves towards the line $x_1 = x_1^*$ and stays there as it continues down the ellipsoid. Also shown in each figure is the phase plot for $xy$ from which the convergence to the line is well displayed.

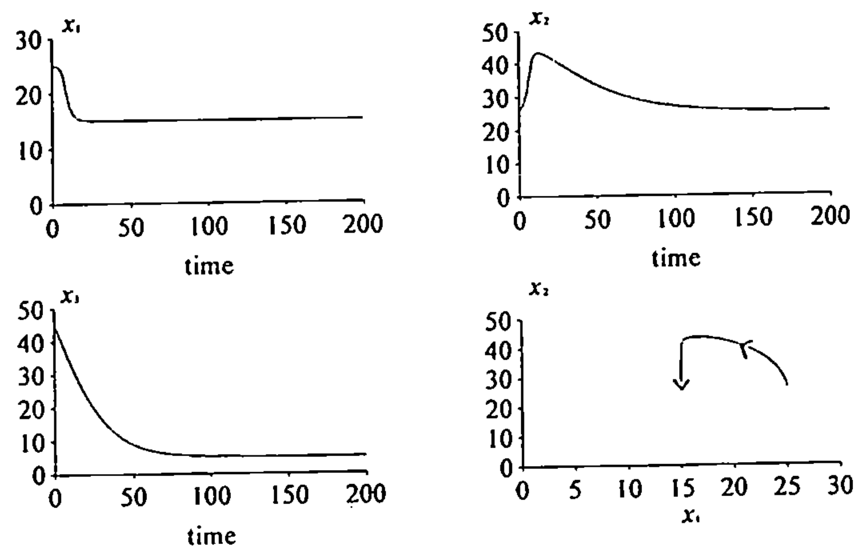


Figure 3.12: Solution curves of Equations 3.22 with $a_1 = 10$, $a_2 = 20$, $a_3 = 40$, $(x_1^*, x_2^*, x_3^*) = (15, 25, 45)$, $\alpha_1 = 0.001$ $\alpha_2 = 0.04$ with a starting point of (24.99,26,25)

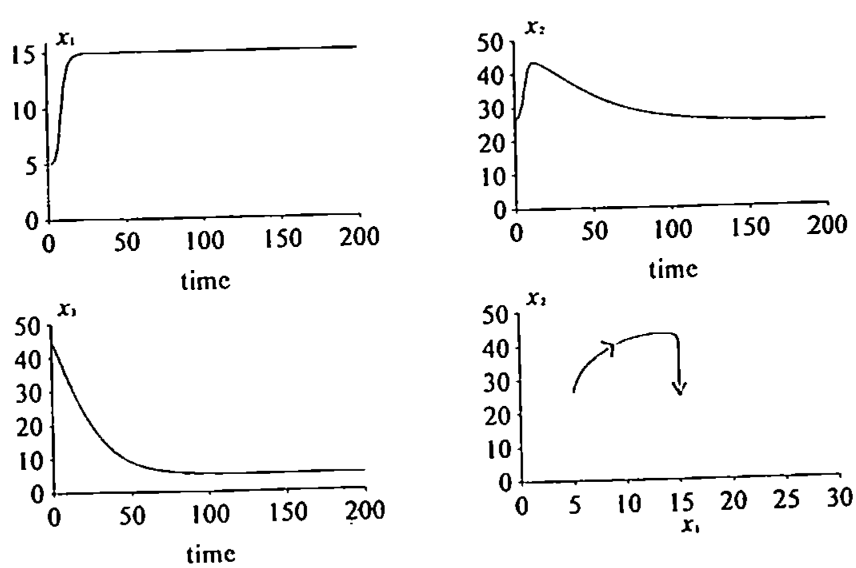


Figure 3.13: Solution curves of Equations 3.22 with $a_1 = 10$, $a_2 = 20$, $a_3 = 40$, $(x_1^*, x_2^*, x_3^*) = (15, 25, 45)$, $\alpha_1 = 0.001$ $\alpha_2 = 0.04$ with a starting point of (5.01,26,45)

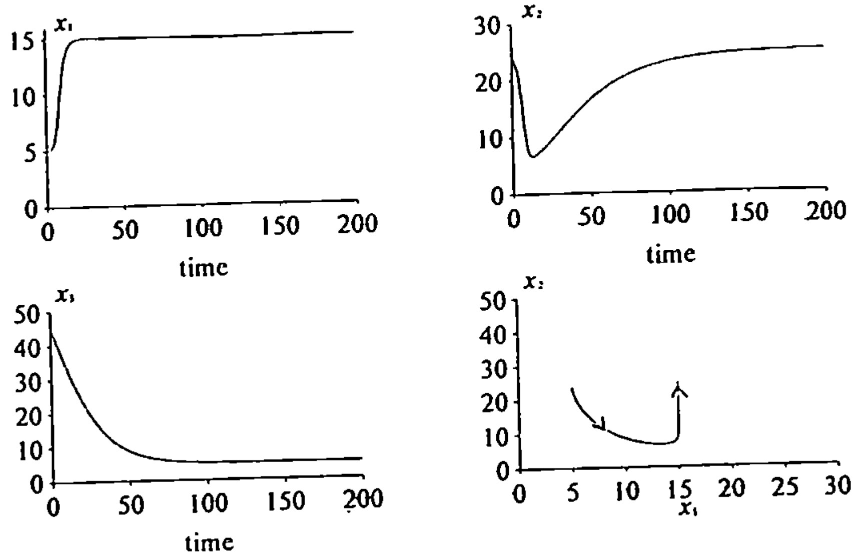


Figure 3.14: Solution curves of Equations 3.22 with $a_1 = 10$, $a_2 = 20$, $a_3 = 40$, $(x_1^*, x_2^*, x_3^*) = (15, 25, 45)$, $\alpha_1 = 0.001$ $\alpha_2 = 0.04$ with a starting point of (5.01,24,45)

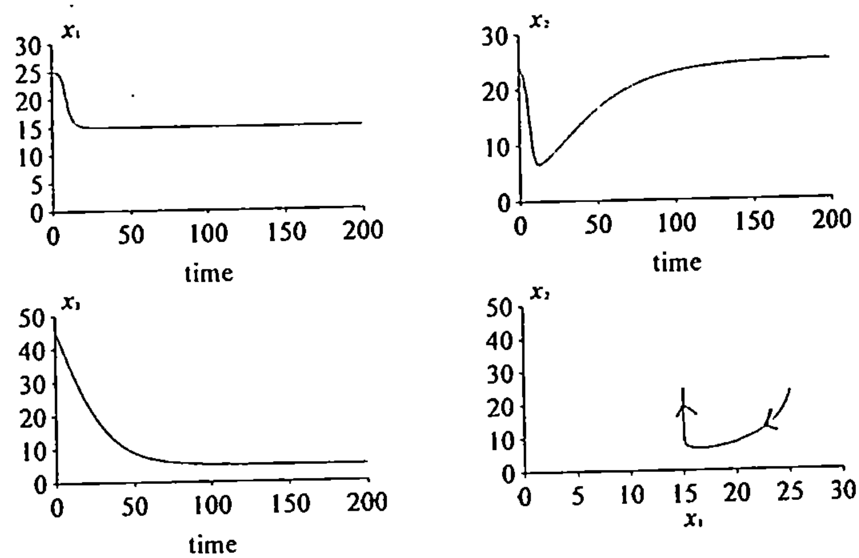


Figure 3.15: Solution curves of Equations 3.22 with $a_1 = 10$, $a_2 = 20$, $a_3 = 40$, $(x_1^*, x_2^*, x_3^*) = (15, 25, 45)$, $\alpha_1 = 0.001$ $\alpha_2 = 0.04$ with a starting point of (24.99,24,45)

#### 3.2.2.3 Model 3

Another choice of $f_1'(t)$ which produces an interesting and distinctive model from Equations 3.10 is another involving $x_1 - x_1^*$ and $x_2 - x_2^*$ as follows.

$$f_1'(t) = (x_1 - x_1^*) + (x_2 - x_2^*) \tag{3.30}$$

$$f_3(t) = 1 \tag{3.31}$$

which produce the following set of differential equations.

$$\frac{dx_1}{dt} = \frac{\alpha_2}{a_3}(x_1 - x_1^*)(x_3 - x_3^*) - \frac{a_1\alpha_1}{a_2}(x_2 - x_2^*)(x_1 - x_1^*) - \frac{a_1\alpha_1}{a_2}(x_2 - x_2^*)^2 \quad (3.32a)$$

$$\frac{dx_2}{dt} = \frac{\alpha_2}{a_3}(x_2 - x_2^*)(x_3 - x_3^*) + \frac{a_2\alpha_1}{a_1}(x_1 - x_1^*)(x_2 - x_2^*) + \frac{a_2\alpha_1}{a_1}(x_1 - x_1^*)^2 \quad (3.32b)$$

$$\frac{dx_3}{dt} = -a_3\alpha_2\left(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}\right) \quad (3.32c)$$

The choice of $f_1(t)$ gives the following equation

$$\int \frac{df_1}{a_1\cos(\alpha_1 f_1(t) + \phi_1) + a_2\sin(\alpha_1 f_1(t) + \phi_1)} = \int \sin(\alpha_2 f_2(t) + \phi_2)dt \quad (3.33)$$

The integration of Equation 3.33 is shown in Appendix A. It has not been possible to obtain an explicit expression for $\alpha_1 f_1(t) + \phi_1$ similar to Equation 3.25 in Model 2. The simplest relationship between $f_1(t)$ and $t$ that has been obtained is

$$\frac{-a_1}{\alpha_1\sqrt{a_1^2 + a_2^2}} \ln\left(\frac{a_1\tan(\frac{\alpha_1 f_1(t)+\phi_1}{2}) - a_2 - \sqrt{a_1^2 + a_2^2}}{a_1\tan(\frac{\alpha_1 f_1(t)+\phi_1}{2}) - a_2 + \sqrt{a_1^2 + a_2^2}}\right) = \frac{2}{\alpha_2}\tan^{-1}(e^{2\alpha_2(t+k_2)}). \quad (3.34)$$

but not much insight can be gained from this complicated expression. Fortunately just as much can be discovered about the solution curves by examining $f_1'(t)$ itself. From Equation 3.30 it follows that

$$\frac{d\theta_1}{dt} = \alpha_1((x_1 - x_1^*) + (x_2 - x_2^*)), \quad (3.35)$$

From this it can be seen that $\theta_1$ will cease to change when

$$(x_1 - x_1^*) + (x_2 - x_2^*) = 0 \quad (3.36)$$

i.e. when

$$x_1 + x_2 = x_1^* + x_2^* \quad (3.37)$$

Therefore as soon as the solutions are such that Equation 3.37 is satisfied then the path will stop circling the ellipsoid. From Equation 3.35, if the starting point is such that

$x_1 + x_2 > x_1^* + x_2^*$ i.e. in section 1 of Figure 3.16 then $\frac{d\theta_1}{dt} > 0$ and therefore $\theta_1$ will increase and travel in an anticlockwise direction around the ellipsoid until it reaches the plane $x_1 + x_2 = x_1^* + x_2^*$ and the path will cease circling. If the starting point is such that $x_1 + x_2 < x_1^* + x_2^*$ i.e. in section 2 of Figure 3.16 then $\frac{d\theta_1}{dt} < 0$ and therefore $\theta_1$ will decrease and travel in an clockwise direction around the ellipsoid until it reaches the plane $x_1 + x_2 = x_1^* + x_2^*$ and the path will cease circling.

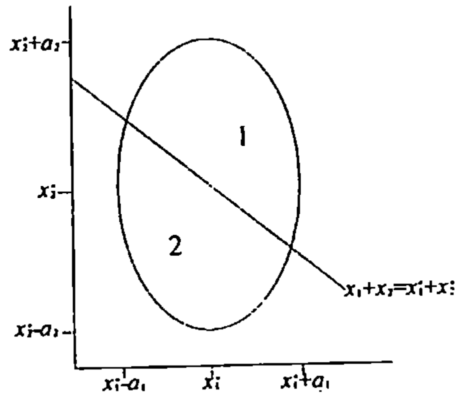


Figure 3.16: $xy$ plane view of the ellipsoid at $x_3 = x_3^*$

Analysis of the fixed points once again shows the fixed points to be $(x_1^*, x_2^*, x_3^* + a_3)$ and $(x_1^*, x_2^*, x_3^* - a_3)$ i.e. the top and bottom of the ellipsoid. The eigenvalues of the matrix $|\mathbf{J} - \lambda\mathbf{I}|$ are found to be $\lambda = \alpha_2$ when evaluated at the point $(x_1^*, x_2^*, x_3^* + a_3)$ and so again this is an unstable fixed point. Similarly with the point $(x_1^*, x_2^*, x_3^* - a_3)$ eigenvalues are $\lambda = -\alpha_2$ and so this point is a stable fixed point.

Therefore with this model the path will travel around and down the ellipsoid until it is such that $x_1 + x_2 = x_1^* + x_2^*$ and then continue to travel down the ellipsoid with $x_1 + x_2 = x_1^* + x_2^*$ towards the point $(x_1^*, x_2^*, x_3^* - a_3)$. A typical curve on the surface of the ellipsoid for this model is shown in Figure 3.17 overleaf

Again this model produces a similar situation to that for Model 2 previously. Equations 3.32 can again be interpreted in terms of an ecosystem consisting of three species $x_1$, $x_2$ and $x_3$, a herbivore, an omnivore and a plant source respectively. This model produces a situation where once the combined herbivore and omnivore population size has reached a

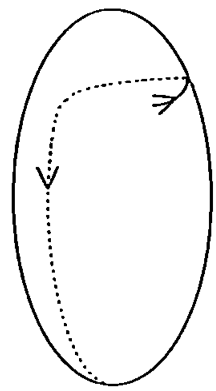

Figure 3.17: A typical solution curve of Equations 3.32

certain level, $x_1^*+x_2^*$, all three populations have settled down to exist together in equilibrium. Therefore this model produces a similar situation to the previous one but this situation is maybe more realistic since it is both the omnivore and herbivore populations that determine the equilibrium state of the populations.

Figures 3.18 to 3.21 show solution curves for Equations 3.32. In each case it can be seen that the path moves towards the line $x_1 + x_2 = x_1^* + x_2^*$ in a direction depending on the starting point. Also shown in each case is the phase plane plot showing the convergence to the line.

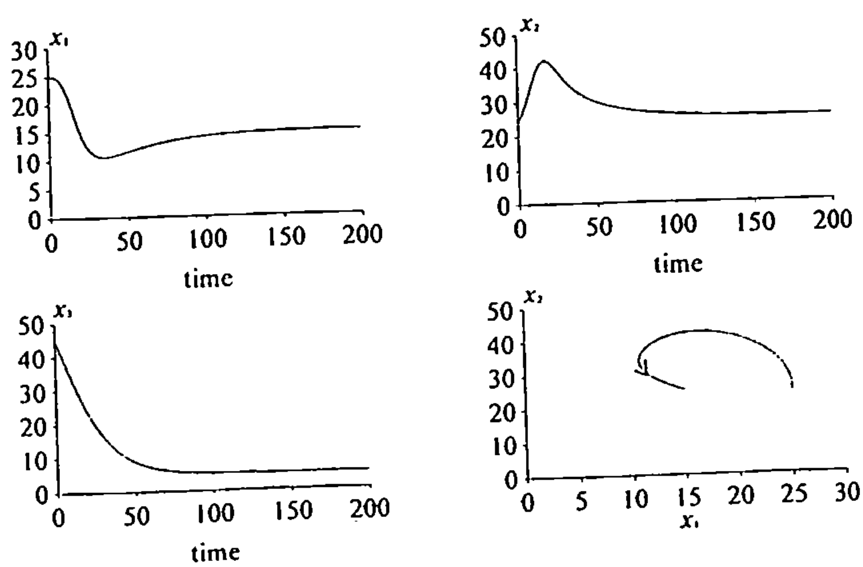


Figure 3.18: Solution curves of Equations 3.32 with $a_1 = 10$, $a_2 = 20$, $a_3 = 40$, $(x_1^*, x_2^*, x_3^*) = (15, 25, 45)$, $\alpha_1 = 0.006$ $\alpha_2 = 0.03$ with a starting point of (24.99,24,45)

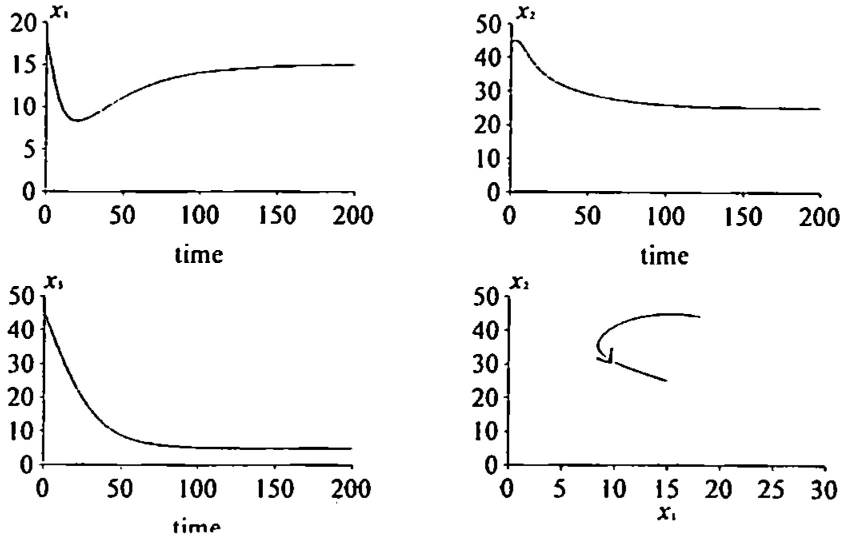


Figure 3.19: Solution curves of Equations 3.32 with $a_1 = 10$, $a_2 = 20$, $a_3 = 40$, $(x_1^*, x_2^*, x_3^*) = (15, 25, 45)$, $\alpha_1 = 0.006$ $\alpha_2 = 0.03$ with a starting point of (18.12,44,45)

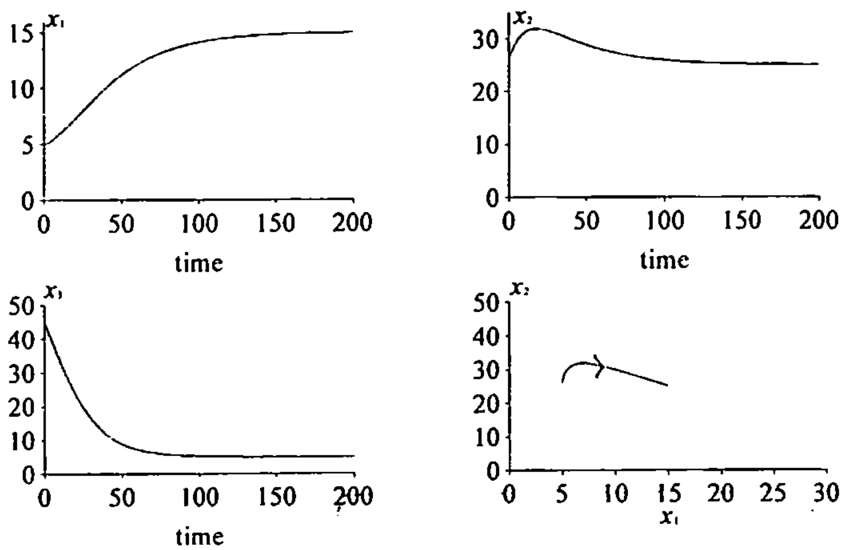


Figure 3.20: Solution curves of Equations 3.32 with $a_1 = 10$, $a_2 = 20$, $a_3 = 40$, $(x_1^*, x_2^*, x_3^*) = (15, 25, 45)$, $\alpha_1 = 0.006$ $\alpha_2 = 0.03$ with a starting point of (5.01,26,45)

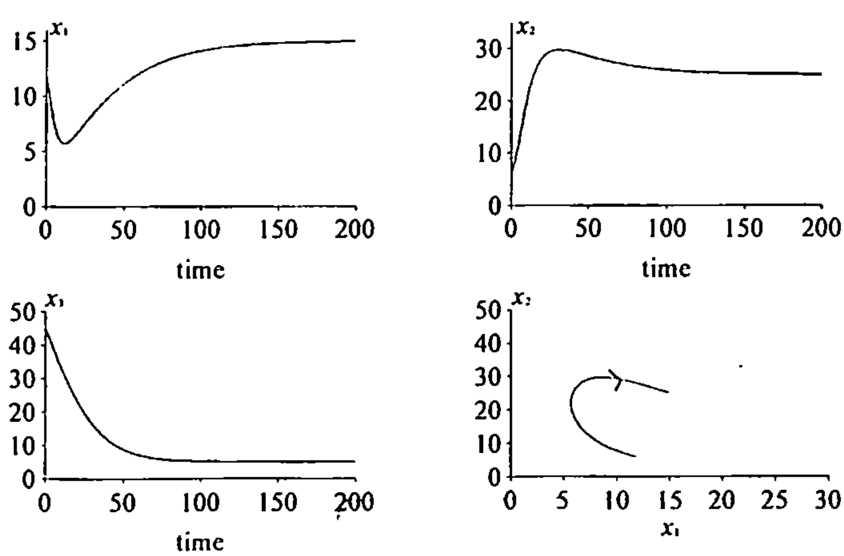


Figure 3.21: Solution curves of Equations 3.32 with $a_1 = 10$, $a_2 = 20$, $a_3 = 40$, $(x_1^*, x_2^*, x_3^*) = (15, 25, 45)$, $\alpha_1 = 0.006$ $\alpha_2 = 0.03$ with a starting point of (11.88,6,45)

### 3.2.3 Summary

Three different models have been discussed here, each one derived from curves embedded on an ellipsoid. There are many more choices of $f_1'(t)$ and $f_3(t)$ that could be made, each producing a different model. However the choices were made here with the aim of keeping the model simple *and* trying to satisfy the conventional criteria for ecosystem models. However, probably the most important feature of each of these three models is how easy it is to picture what is happening to the path on the surface. The technique allows a three–dimensional picture to be built up thus showing all three variables interacting with each other rather than the usual method of trying to interpret three different time series plots which is often difficult.

Having given this fairly detailed analysis of the models produced by using the ellipsoid as a basis enables a generalisation to a higher dimensional approach to take place. By extending the knowledge learnt here the theory can be applied to include spaces of higher dimensions thus increasing the scope of this geometric approach to modelling interacting populations. In the following section the analysis is extended to four variables and a four–dimensional 'ellipsoid' is considered.

## 3.3 Four–dimensional 'Ellipsoid'

### 3.3.1 Formulating the Model

Building on from the three–dimensional ellipsoid in the previous section the general equation for a four–dimensional shape of the same form is

$$\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2} + \frac{(x_4 - x_4^*)^2}{a_4^2} = 1. \tag{3.38}$$

where, as before, $a_1$, $a_2$, $a_3$ and $a_4$ are the characteristic parameters, $(x_1^*, x_2^*, x_3^*, x_4^*)$ is the 'centre' of the shape and the four variables are $x_1$, $x_2$, $x_3$ and $x_4$. Equation 3.38 can be parameterized along the same lines as the three variable ellipsoid in the last section. This time there are three parameters $\theta_1$, $\theta_2$ and $\theta_3$. It is difficult to describe these parameters in terms of angles since a four dimensional shape cannot be visualised but an informal description could be as follows: $\theta_1$ is an indication of how the path moves around the $x_1$ axis, $\theta_2$ is an indication of how the path moves around the $x_3$ axis and $\theta_3$ is an indication of how the path moves around the $x_4$ axis. Therefore a possible parameterization of Equation 3.38 consistent with this interpretation will be

$$x_1 - x_1^* = a_1 \sin\theta_3 \sin\theta_2 \cos\theta_1 \tag{3.39a}$$

$$x_2 - x_2^* = a_2 \sin\theta_3 \sin\theta_2 \sin\theta_1 \tag{3.39b}$$

$$x_3 - x_3^* = a_3 \sin\theta_3 \cos\theta_2 \tag{3.39c}$$

$$x_4 - x_4^* = a_4 \cos\theta_3. \tag{3.39d}$$

By letting $\theta_1 = \alpha_1 f_1(t) + \phi_1$, $\theta_2 = \alpha_2 f_2(t) + \phi_2$ and $\theta_3 = \alpha_3 f_3(t) + \phi_3$ a set of parametric equations for Equations 3.38 is

$$x_1 - x_1^* = a_1 \sin(\alpha_3 f_3(t) + \phi_3) \sin(\alpha_2 f_2(t) + \phi_2) \cos(\alpha_1 f_1(t) + \phi_1) \tag{3.40a}$$

$$x_2 - x_2^* = a_2 \sin(\alpha_3 f_3(t) + \phi_3) \sin(\alpha_2 f_2(t) + \phi_2) \sin(\alpha_1 f_1(t) + \phi_1) \tag{3.40b}$$

$$x_3 - x_3^* = a_3 \sin(\alpha_3 f_3(t) + \phi_3) \cos(\alpha_2 f_2(t) + \phi_2) \tag{3.40c}$$

$$x_4 - x_4^* = a_4 \cos(\alpha_3 f_3(t) + \phi_3). \tag{3.40d}$$

Now differentiating Equations 3.40 with respect to $t$ gives the resulting set of differential equations.

$$\begin{aligned}\frac{dx_1}{dt} = {} & \cos(\alpha_1 f_1(t) + \phi_1)[a_1 \alpha_2 f_2'(t) \cos(\alpha_2 f_2(t) + \phi_2) \sin(\alpha_3 f_3(t) + \phi_3) \\ & + a_1 \alpha_3 f_3'(t) \sin(\alpha_2 f_2(t) + \phi_2) \cos(\alpha_3 f_3(t) + \phi_3)] \\ & - a_1 \alpha_1 f_1'(t) \sin(\alpha_1 f_1(t) + \phi_1) \sin(\alpha_2 f_2(t) + \phi_2) \sin(\alpha_3 f_3(t) + \phi_3)\end{aligned} \tag{3.41a}$$

$$\frac{dx_2}{dt} = \sin(\alpha_1 f_1(t) + \phi_1)[a_2\alpha_2 f_2'(t)\cos(\alpha_2 f_2(t) + \phi_2)\sin(\alpha_3 f_3(t) + \phi_3)$$
$$+a_2\alpha_3 f_3'(t)\sin(\alpha_2 f_2(t) + \phi_2)\cos(\alpha_3 f_3(t) + \phi_3)]$$
$$+a_2\alpha_1 f_1'(t)\cos(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_2 f_2(t) + \phi_2)\sin(\alpha_3 f_3(t) + \phi_3) \quad (3.41b)$$

$$\frac{dx_3}{dt} = a_3\alpha_3 f_3'(t)\cos(\alpha_2 f_2(t) + \phi_2)\cos(\alpha_3 f_3(t) + \phi_3)$$
$$-a_3\alpha_2 f_2'(t)\sin(\alpha_2 f_2(t) + \phi_2)\sin(\alpha_3 f_3(t) + \phi_3) \quad (3.41c)$$

$$\frac{dx_4}{dt} = -a_4\alpha_3 f_3'(t)\sin(\alpha_3 f_3(t) + \phi_3). \quad (3.41d)$$

By using Equations 3.38, 3.40 and the identity $\sin^2\Theta + \cos^2\Theta = 1$ the following expressions for $\sin(\alpha_1 f_1(t) + \phi_1)$, $\cos(\alpha_1 f_1(t) + \phi_1)$, etc. can be obtained.

$$\sin(\alpha_1 f_1(t) + \phi_1) = \frac{x_2 - x_2^*}{a_2\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2}}} \quad (3.42a)$$

$$\cos(\alpha_1 f_1(t) + \phi_1) = \frac{x_1 - x_1^*}{a_1\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2}}} \quad (3.42b)$$

$$\sin(\alpha_2 f_2(t) + \phi_2) = \frac{\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2}}}{\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2} + \frac{(x_3-x_3^*)^2}{a_3^2}}} \quad (3.42c)$$

$$\cos(\alpha_2 f_2(t) + \phi_2) = \frac{x_3 - x_3^*}{a_3\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2} + \frac{(x_3-x_3^*)^2}{a_3^2}}} \quad (3.42d)$$

$$\sin(\alpha_3 f_3(t) + \phi_3) = \sqrt{\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2}} \quad (3.42e)$$

$$\cos(\alpha_3 f_3(t) + \phi_3) = \frac{x_4 - x_4^*}{a_4}. \quad (3.42f)$$

The similarities between the formulation of the three–dimensional model and this one can already be seen when comparing the above equations to those for the same steps in the three–dimensional case (Equations 3.6).

The substitution of Equations 3.42 into Equations 3.41 therefore produces the following set of equations.

$$\frac{dx_1}{dt} = \frac{\alpha_2 f_2'(x_1 - x_1^*)(x_3 - x_3^*)}{a_3\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2}}} + \frac{\alpha_3 f_3'(t)(x_1 - x_1^*)(x_4 - x_4^*)}{a_4\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2} + \frac{(x_3-x_3^*)^2}{a_3^2}}}$$

$$-\frac{a_1\alpha_1 f_1'(t)(x_2 - x_2^*)}{a_2} \tag{3.43a}$$

$$\frac{dx_2}{dt} = \frac{\alpha_2 f_2'(t)(x_2 - x_2^*)(x_3 - x_3^*)}{a_3\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2}}} + \frac{\alpha_3 f_3'(t)(x_2 - x_2^*)(x_4 - x_4^*)}{a_4\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2} + \frac{(x_3-x_3^*)^2}{a_3^2}}}$$

$$+\frac{a_2\alpha_1 f_1'(t)(x_1 - x_1^*)}{a_1} \tag{3.43b}$$

$$\frac{dx_3}{dt} = \frac{\alpha_3 f_3'(t)(x_3 - x_3^*)(x_4 - x_4^*)}{\sqrt{\frac{(x_1-x_1^*)^2}{a_1^2} + \frac{(x_2-x_2^*)^2}{a_2^2} + \frac{(x_3-x_3^*)^2}{a_3^2}}} - a_3\alpha_2 f_2'(t)\sqrt{\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}} \tag{3.43c}$$

$$\frac{dx_4}{dt} = -a_4\alpha_3 f_3'(t)\sqrt{\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2}}. \tag{3.43d}$$

Equations 3.43 therefore model a four variable system whose solutions are such that

$$\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2} + \frac{(x_4 - x_4^*)^2}{a_4^2} = 1. \tag{3.44}$$

As in the three-dimensional case, there are numerous choices of functions which can be made for $f_1(t)$, $f_2(t)$ and $f_3(t)$. However visualising what happens to the path will be more difficult. Therefore examination of the parameters $\theta_1$, $\theta_2$ and $\theta_3$ will be more informative. Also analysis of the fixed points will reveal the final position of the path. Therefore the skills learnt in the 3-dimensional case, where visualising the surface made interpretation easier, can now be used to good effect in these higher dimensions.

### 3.3.2 Many Models From One

By using similar arguments to those in the three variable model, choices for $f_2'(t)$ and $f_3'(t)$ can be made to simplify the above set of equations into one which resembles a real situation. Therefore by letting

$$f_2'(t) = f_4(t)\sqrt{\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}} \tag{3.45}$$

$$f_3'(t) = f_5(t)\sqrt{\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2}} \tag{3.46}$$

Equations 3.43 become

$$\begin{aligned}
\frac{dx_1}{dt} &= \frac{\alpha_2 f_4(t)}{a_3}(x_1 - x_1^*)(x_3 - x_3^*) + \frac{\alpha_3 f_5(t)}{a_4}(x_1 - x_1^*)(x_4 - x_4^*) \\
&\quad - \frac{a_1 \alpha_1 f_1'(t)}{a_2}(x_2 - x_2^*) && \text{(3.47a)} \\
\frac{dx_2}{dt} &= \frac{\alpha_2 f_4(t)}{a_3}(x_2 - x_2^*)(x_3 - x_3^*) + \frac{\alpha_3 f_5(t)}{a_4}(x_2 - x_2^*)(x_4 - x_4^*) \\
&\quad + \frac{a_2 \alpha_1 f_1'(t)}{a_1}(x_1 - x_1^*) && \text{(3.47b)} \\
\frac{dx_3}{dt} &= \frac{\alpha_3 f_5(t)}{a_4}(x_3 - x_3^*)(x_4 - x_4^*) - a_3 \alpha_2 f_4(t)\left(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}\right) && \text{(3.47c)} \\
\frac{dx_4}{dt} &= -a_4 \alpha_3 f_5(t)\left(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2}\right). && \text{(3.47d)}
\end{aligned}$$

This set of differential equations form the basic equations for a four dimensional model. There are numerous choices that can be made for the three functions $f_1'(t)$, $f_4(t)$ and $f_5(t)$, many more in fact than for the three-dimensional case. Three of the options are examined in detail below using similar substitutions to those made in the three-dimensional model to facilitate comparison.

#### 3.3.2.1 Model 1

This first model is the simplest model in that all the functions $f_1'$, $f_4$ and $f_5$ are constant i.e.

$$f_1'(t) = 1, \tag{3.48a}$$

$$f_4(t) = 1, \tag{3.48b}$$

$$f_5(t) = 1. \tag{3.48c}$$

Therefore the model is

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = \frac{\alpha_2}{a_3}(x_1 - x_1^*)(x_3 - x_3^*) + \frac{\alpha_3}{a_4}(x_1 - x_1^*)(x_4 - x_4^*) - \frac{a_1\alpha_1}{a_2}(x_2 - x_2^*) \tag{3.49a}$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = \frac{\alpha_2}{a_3}(x_2 - x_2^*)(x_3 - x_3^*) + \frac{\alpha_3}{a_4}(x_2 - x_2^*)(x_4 - x_4^*) + \frac{a_2\alpha_1}{a_1}(x_1 - x_1^*) \tag{3.49b}$$

$$\frac{\mathrm{d}x_3}{\mathrm{d}t} = \frac{\alpha_3}{a_4}(x_3 - x_3^*)(x_4 - x_4^*) - a_3\alpha_2(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}) \tag{3.49c}$$

$$\frac{\mathrm{d}x_4}{\mathrm{d}t} = -a_4\alpha_3(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2}). \tag{3.49d}$$

The first step in analysing how the path behaves is to analyse the fixed points. The fixed points of the system governed by Equations 3.49 occur when $\frac{\mathrm{d}x_i}{\mathrm{d}t} = 0$, $i = 1 \ldots 4$. Using a similar principle to that in Section 3.2 for the three–dimensional case the fixed points of this system are found to be $(x_1^*, x_2^*, x_3^*, x_4^* + a_4)$ and $(x_1^*, x_2^*, x_3^*, x_4^* - a_4)$.

To investigate the stability of these fixed points the Jacobian matrix for Equations 3.49 is found to be

$$\mathbf{J} = \begin{bmatrix} \frac{\alpha_2(x_3-x_3^*)}{a_3} + \frac{\alpha_3(x_4-x_4^*)}{a_4} & -\frac{a_1\alpha_1}{a_2} & \frac{\alpha_2(x_1-x_1^*)}{a_3} & \frac{\alpha_3(x_1-x_1^*)}{a_4} \\ \frac{a_2\alpha_1}{a_1} & \frac{\alpha_2(x_3-x_3^*)}{a_3} + \frac{\alpha_3(x_4-x_4^*)}{a_4} & \frac{\alpha_2(x_2-x_2^*)}{a_3} & \frac{\alpha_3(x_2-x_2^*)}{a_4} \\ \frac{-2a_3\alpha_2(x_1-x_1^*)}{a_1^2} & \frac{-2a_3\alpha_2(x_2-x_2^*)}{a_2^2} & \frac{\alpha_3(x_4-x_4^*)}{a_4} & \frac{\alpha_3(x_4-x_4^*)}{a_4} \\ \frac{-2a_4\alpha_3(x_1-x_1^*)}{a_1^2} & \frac{-2a_4\alpha_3(x_2-x_2^*)}{a_2^2} & \frac{-2a_4\alpha_3(x_3-x_3^*)}{a_3^2} & 0 \end{bmatrix} \tag{3.50}$$

which when evaluated at the fixed point $x_1 = x_1^*$, $x_2 = x_2^*$, $x_3 = x_3^*$, $x_4 = x_4^* + a_4$ produces the extremely simple matrix

$$\mathbf{J} = \begin{bmatrix} \alpha_3 & -\frac{a_1\alpha_1}{a_2} & 0 \\ \frac{a_2\alpha_1}{a_1} & \alpha_3 & 0 \\ 0 & 0 & \alpha_3 \end{bmatrix} \tag{3.51}$$

Solving $|\mathbf{J} - \lambda\mathbf{I}|$ for the eigenvalues $\lambda$, gives $\lambda = \alpha_3$, $\alpha_3 + i\alpha_1$ and $\alpha_3 - i\alpha_1$. Therefore, since the eigenvalues have positive real parts, this fixed point is an unstable one. Similar analysis for the fixed point $x_1 = x_1^*$, $x_2 = x_2^*$, $x_3 = x_3^*$, $x_4 = x_4^* - a_4$ gives its eigenvalues to be $\lambda = -\alpha_3$, $-\alpha_3 + i\alpha_1$ and $-\alpha_3 - i\alpha_1$ and so this is a stable fixed point. Therefore any path will tend to travel away from the point $(x_1^*, x_2^*, x_3^*, x_4^* + a_4)$ towards the point $(x_1^*, x_2^*, x_3^*, x_4^* - a_4)$ and once there will remain there. Therefore the $x_4$ component will behave in a similar manner to the $x_3$ component of the three variable system in that it will gradually decrease until it reaches the point $x_4^* - a_4$.

Analysis of the three parameters $\theta_1$, $\theta_2$ and $\theta_3$ may provide some insight on how the path behaves. Integrating $f_1'(t)$, $f_2'(t)$ and $f_3'(t)$ with respect to $t$ the following are obtained:- (Details of the integration are shown in Appendix A.)

$$\theta_1 = \alpha_1(t + k_1) + \phi_1 \tag{3.52a}$$

$$\theta_2 = 2\tan^{-1}\Big(\exp[\frac{2\alpha_2}{\alpha_3}(\tan^{-1}[\exp(\alpha_3(t + k_3))])]\Big) \tag{3.52b}$$

$$\theta_3 = 2\tan^{-1}(e^{\alpha_3(t+k_3)}) \tag{3.52c}$$

Therefore, as time $t$ increases, $\theta_1$ increases without limit in a similar fashion to the $\theta_1$ in to Model 1 in the three–dimensional case. Therefore, since $\theta_1$ governs the behaviour of $x_1$ and $x_2$, the time series plots for $x_1$ and $x_2$ will be similar to those for $x_1$ and $x_2$ in Model 1 of the ellipsoid (Section 3.2.2.1). The movement of the path in the $x_4$ direction will be similar to that of the $x_3$ path in the ellipsoid since the stability analysis determines that the direction of the travel is in the 'downwards' direction of the $x_4$ axis. The movement of the path in the $x_3$ direction is governed by $\theta_2$ and is a little more difficult to picture. As $t \to \infty$, and since $\theta_2$ is an increasing function of $t$, $\theta_2 \to \pi$. This means that the path will move around the $x_3$ axis with an increasing angle until the angle equals $\pi$ and then remain constant.

Equations 3.49 could now be interpreted in terms of an ecosystem consisting of four species $x_1$, $x_2$, $x_3$ and $x_4$.

- $x_1$ grows from the presence of $x_3$ and $x_4$ and dies from the presence of $x_2$.
- $x_2$ grows from the presence of $x_1$, $x_3$ and $x_4$.
- $x_3$ grows from the presence of $x_4$ and dies from the presence of $x_1$ and $x_2$.
- $x_4$ dies from the presence of $x_1$, $x_2$ and $x_3$.

This system can therefore be described as consisting of a dominant omnivore, $x_2$, an omnivore, $x_1$, a herbivore, $x_3$, and a plant source, $x_4$. So, comparing it to the ecosystem modelled by the three–dimensional case, adding another dimension has had the effect of adding another member, an omnivore, to the food chain.

The three parameters $\alpha_1$, $\alpha_2$ and $\alpha_3$ determine the 'speed' at which the path travels over the surface and can be interpreted as the rates of interaction, growth or death of the four members of the ecosystem. $\alpha_1$ is proportional to the rate at which the two omnivores interact with each other and therefore is proportional to the number of fluctuations over time for the omnivore and the dominant omnivore. $\alpha_2$ is proportional to the rate of interaction of both omnivores with the herbivore and therefore is proportional the rate of decay of herbivore. Similarly $\alpha_3$ is proportional to the rate of decay of the plant source since it represents the rate of interaction between the plant source and the other three members of the ecosystem. All four populations settle down to an equilibrium as in the three variable ecosystem modelled by Model 1 previously.

Time series plots are given in Figures 3.22 to 3.25 showing the effect of different parameter values.

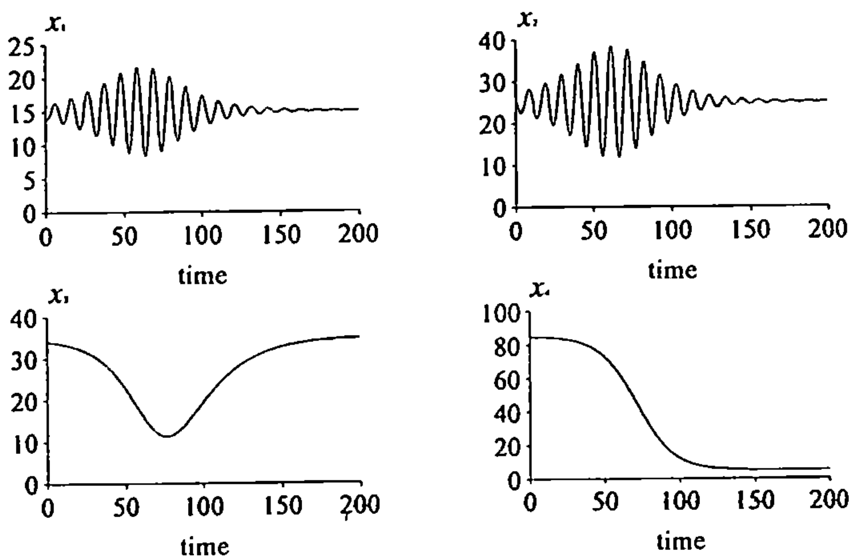


Figure 3.22: Solution curves of Equations 3.49 with $a_1 = 10$, $a_2 = 20$, $a_3 = 30$, $a_4 = 40$, $(x_1^*, x_2^*, x_3^*, x_4^*) = (15, 25, 35, 45)$, $\alpha_1 = 0.6$, $\alpha_2 = 0.02$ and $\alpha_3 = 0.04$

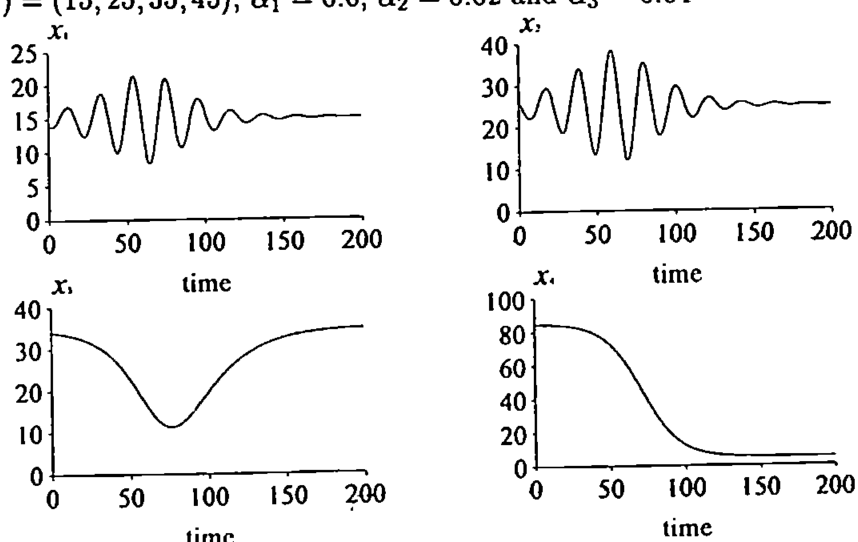


Figure 3.23: Solution curves of Equations 3.49 with $a_1 = 10$, $a_2 = 20$, $a_3 = 30$, $a_4 = 40$, $(x_1^*, x_2^*, x_3^*, x_4^*) = (15, 25, 35, 45)$, $\alpha_1 = 0.3$, $\alpha_2 = 0.02$ and $\alpha_3 = 0.04$

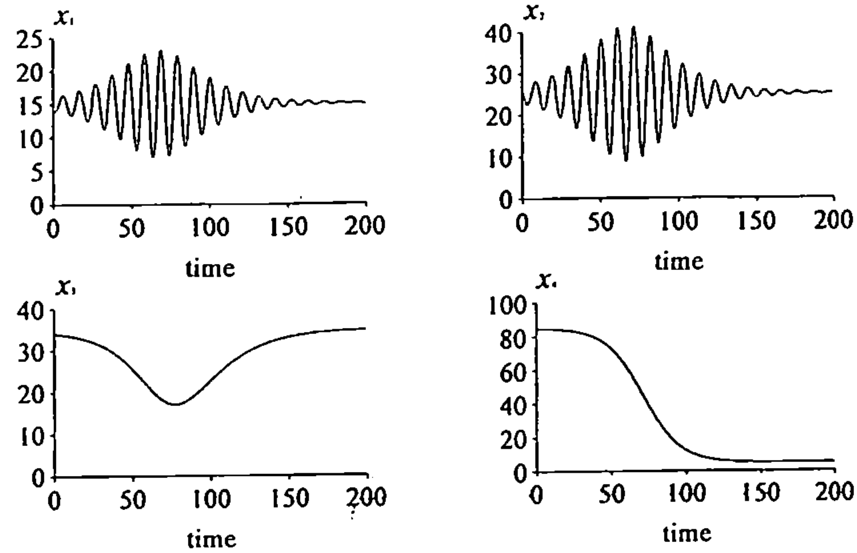


Figure 3.24: Solution curves of Equations 3.49 with $a_1 = 10$, $a_2 = 20$, $a_3 = 30$, $a_4 = 40$, $(x_1^*, x_2^*, x_3^*, x_4^*) = (15, 25, 35, 45)$, $\alpha_1 = 0.6$, $\alpha_2 = 0.01$ and $\alpha_3 = 0.04$

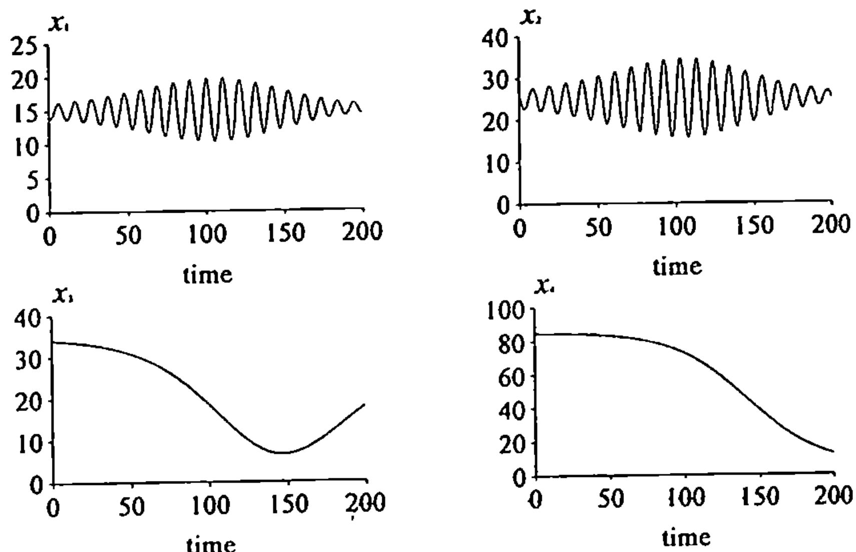


Figure 3.25: Solution curves of Equations 3.49 with $a_1 = 10$, $a_2 = 20$, $a_3 = 30$, $a_4 = 40$, $(x_1^*, x_2^*, x_3^*, x_4^*) = (15, 25, 35, 45)$, $\alpha_1 = 0.6$, $\alpha_2 = 0.02$ and $\alpha_3 = 0.02$

#### 3.3.2.2 Model 2

Again the choice here is such that the model includes an $x_1 x_2$ term to represent the interaction between these two variables. Therefore the choice of $f_1'(t)$ is

$$f_1' = (x_1 - x_1^*)(x_2 - x_2^*). \tag{3.53}$$

By letting $f_4(t)$ and $f_5(t)$ remain equal to 1 the model becomes

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = \frac{\alpha_2}{a_3}(x_1 - x_1^*)(x_3 - x_3^*) + \frac{\alpha_3}{a_4}(x_1 - x_1^*)(x_4 - x_4^*)$$

$$-\frac{a_1\alpha_1}{a_2}(x_2 - x_2^*)^2(x_1 - x_1^*) \tag{3.54a}$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = \frac{\alpha_2}{a_3}(x_2 - x_2^*)(x_3 - x_3^*) + \frac{\alpha_3}{a_4}(x_2 - x_2^*)(x_4 - x_4^*)$$

$$+\frac{a_2\alpha_1}{a_1}(x_1 - x_1^*)^2(x_2 - x_2^*) \tag{3.54b}$$

$$\frac{\mathrm{d}x_3}{\mathrm{d}t} = \frac{\alpha_3}{a_4}(x_3 - x_3^*)(x_4 - x_4^*) - a_3\alpha_2\left(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}\right) \tag{3.54c}$$

$$\frac{\mathrm{d}x_4}{\mathrm{d}t} = -a_4\alpha_3\left(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2}\right). \tag{3.54d}$$

In this model the fixed points are again found to be $(x_1^*, x_2^*, x_3^*, x_4^* + a_4)$ and $(x_1^*, x_2^*, x_3^*, x_4^* - a_4)$. Analysis of the Jacobian matrix once again determines that $(x_1^*, x_2^*, x_3^*, x_4^* + a_4)$ is an unstable fixed point and that $(x_1^*, x_2^*, x_3^*, x_4^* - a_4)$ is a stable one. Therefore this family of models all behave in a similar manner when comparing the movement of the path on the surface.

In this model $\theta_2$ and $\theta_3$ are the same as for Model 1 but it has not been possible to find an explicit expression for $\theta_1$ by integration. However by examining $\frac{\mathrm{d}\theta_1}{\mathrm{d}t}$ i.e.

$$\frac{\mathrm{d}\theta_1}{\mathrm{d}t} = \alpha_1(x_1 - x_1^*)(x_2 - x_2^*) \tag{3.55}$$

it can be seen that $\theta_1$ will behave in a similar manner to the $\theta_1$ in Model 2 of the three–dimensional ellipsoid (see Section 3.2.2.2). The path on the surface will move in such a way so that it will always approach the line $x_1 = x_1^*$. The value of the starting point (especially the $x_1$ and the $x_2$ value) will determine the direction of the path around the surface. If $x_1 > x_1^*$ and $x_2 > x_2^*$ or $x_1 < x_1^*$ and $x_2 < x_2^*$ then the path moves in an anticlockwise direction with respect to the $x_1$ axis. If $x_1 < x_1^*$ and $x_2 > x_2^*$ or $x_1 > x_1^*$ and $x_2 < x_2^*$ then the path moves in a clockwise direction with respect to the $x_1$ axis.

Therefore the model described by Equations 3.54 may again be applied to a four variable ecosystem consisting of a omnivore, $x_1$, a dominant omnivore, $x_2$, a herbivore $x_3$, and a plant source, $x_4$. However, this model produces a situation where once the omnivore, $x_1$, has reached a certain level, $x_1^*$, its natural growth rate is matched by its death rate. The fluctuations produced in Model 1 do not occur and all four populations quickly settle down to exist together in equilibrium as in the comparable model for the three varaible ecosystem. This convergence of $x_1$ to $x_1^*$ can be seen from the phase plane plot of $x_1x_2$ which is shown below in Figures 3.26 to 3.29 along with the time series plots for four different starting points.

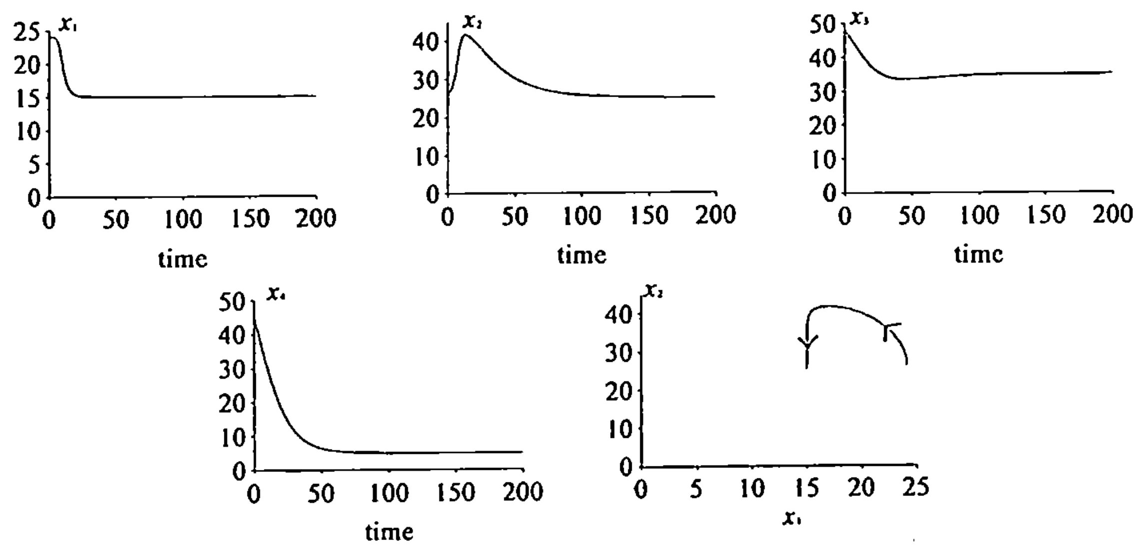


Figure 3.26: Solution curves of Equations 3.54 with $a_1 = 10$, $a_2 = 20$, $a_3 = 30$, $a_4 = 40$, $(x_1^*, x_2^*, x_3^*, x_4^*) = (15, 25, 35, 45)$, $\alpha_1 = 0.002$, $\alpha_2 = 0.02$ and $\alpha_3 = 0.04$ with a starting point of $(24, 26, 48, 45)$

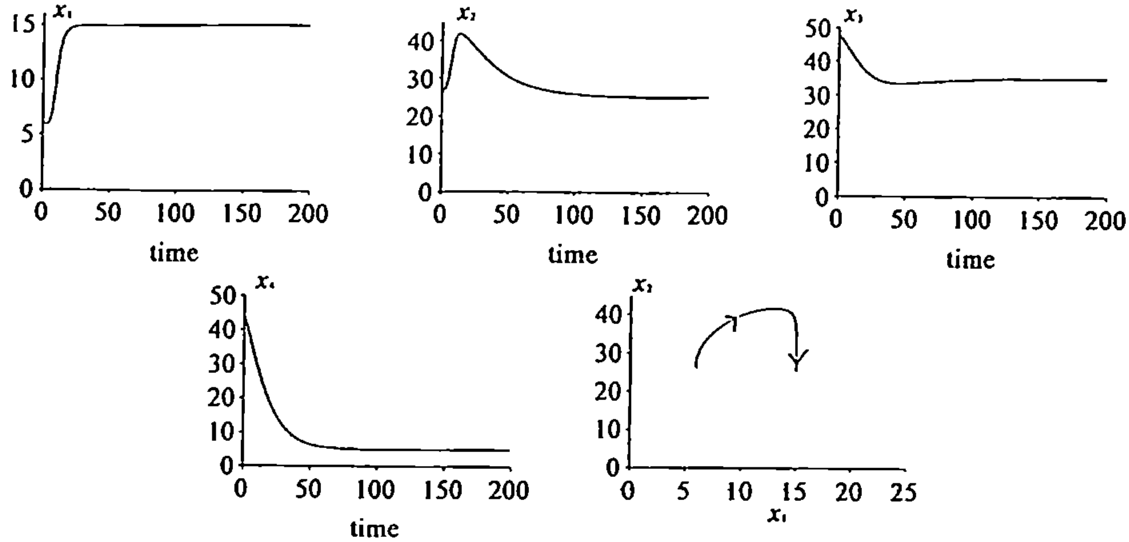

Figure 3.27: Solution curves of Equations 3.54 with $a_1 = 10$, $a_2 = 20$, $a_3 = 30$, $a_4 = 40$, $(x_1^*, x_2^*, x_3^*, x_4^*) = (15, 25, 35, 45)$, $\alpha_1 = 0.002$, $\alpha_2 = 0.02$ and $\alpha_3 = 0.04$ with a starting point of $(4, 26, 48, 45)$

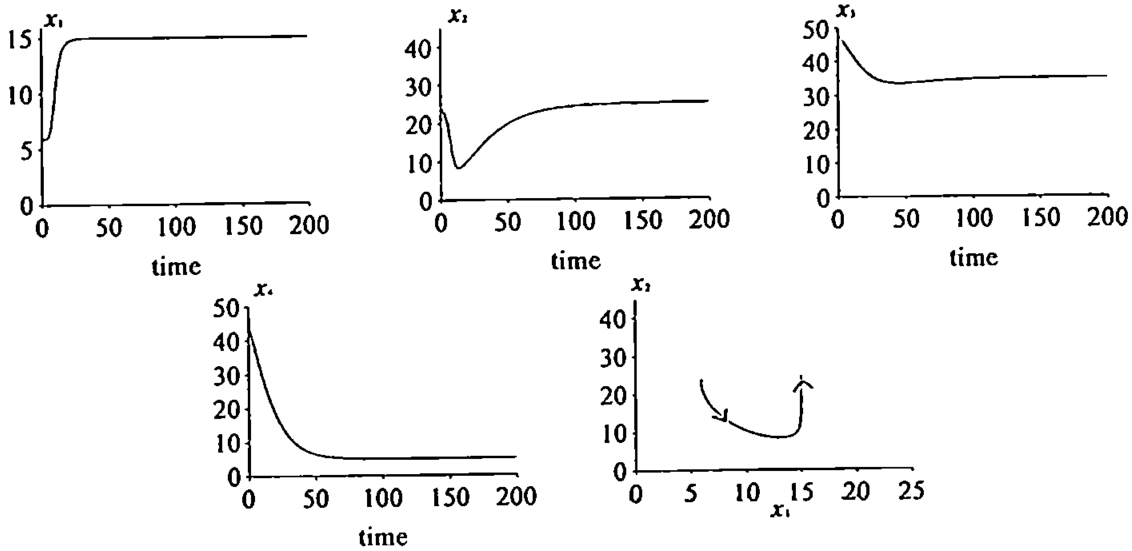

Figure 3.28: Solution curves of Equations 3.54 with $a_1 = 10$, $a_2 = 20$, $a_3 = 30$, $a_4 = 40$, $(x_1^*, x_2^*, x_3^*, x_4^*) = (15, 25, 35, 45)$, $\alpha_1 = 0.002$, $\alpha_2 = 0.02$ and $\alpha_3 = 0.04$ with a starting point of $(6, 24, 48, 45)$

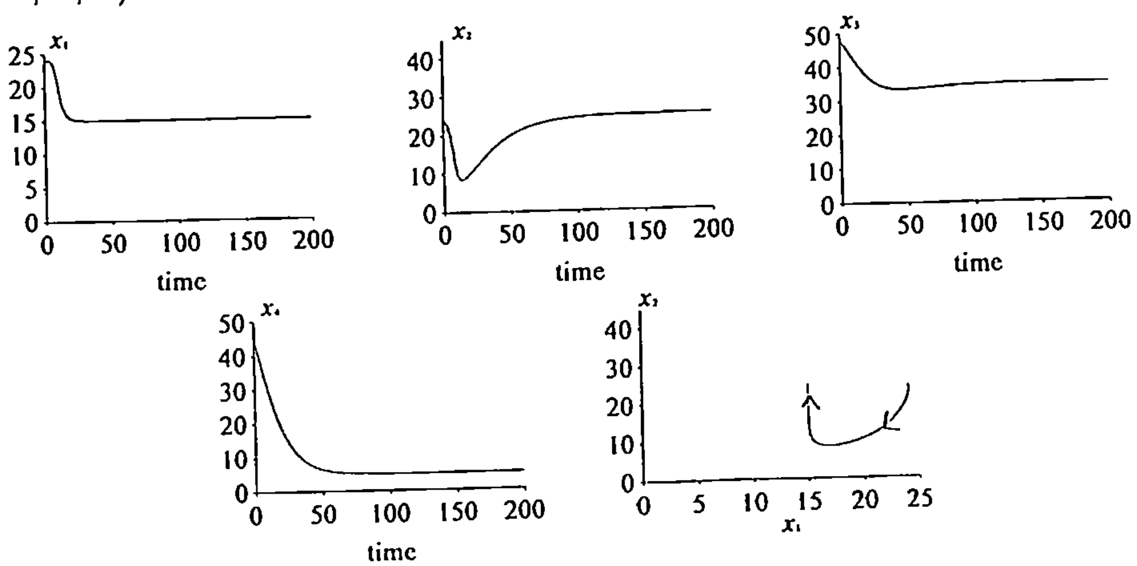

Figure 3.29: Solution curves of Equations 3.54 with $a_1 = 10$, $a_2 = 20$, $a_3 = 30$, $a_4 = 40$, $(x_1^*, x_2^*, x_3^*, x_4^*) = (15, 25, 35, 45)$, $\alpha_1 = 0.002$, $\alpha_2 = 0.02$ and $\alpha_3 = 0.04$ with a starting point of $(24, 24, 48, 45)$

#### 3.3.2.3 Model 3

This third model introduces an $x_1x_2$ term similar to the three dimensional case by allowing

$$f_1'(t) = (x_1 - x_1^*) + (x_2 - x_2^*) \tag{3.56}$$

and the model in this case is

$$\begin{aligned}
\frac{dx_1}{dt} &= \frac{\alpha_2}{a_3}(x_1 - x_1^*)(x_3 - x_3^*) + \frac{\alpha_3}{a_4}(x_1 - x_1^*)(x_4 - x_4^*) \\
&\quad -\frac{a_1\alpha_1}{a_2}(x_2 - x_2^*)(x_1 - x_1^*) - \frac{a_1\alpha_1}{a_2}(x_2 - x_2^*)^2
\end{aligned} \tag{3.57a}$$

$$\begin{aligned}
\frac{dx_2}{dt} &= \frac{\alpha_2}{a_3}(x_2 - x_2^*)(x_3 - x_3^*) + \frac{\alpha_3}{a_4}(x_2 - x_2^*)(x_4 - x_4^*) \\
&\quad +\frac{a_2\alpha_1}{a_1}(x_1 - x_1^*)(x_2 - x_2^*) + \frac{a_2\alpha_1}{a_1}(x_1 - x_1^*)^2
\end{aligned} \tag{3.57b}$$

$$\frac{dx_3}{dt} = \frac{\alpha_3}{a_4}(x_3 - x_3^*)(x_4 - x_4^*) - a_3\alpha_2\left(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}\right) \tag{3.57c}$$

$$\frac{dx_4}{dt} = -a_4\alpha_3\left(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2}\right). \tag{3.57d}$$

Here it is quite easy to see that this model will behave in a similar manner to Model 3 for the ellipsoid. The paths will move 'down' the surface and settle down to $(x_1^*, x_2^*, x_3^*, x_4^* - a_4)$. Since the analysis of $\theta_1$ is the same as for that of Model 3 for the ellipsoid the behaviour of it is the same and the path on the surface will always approach the point $x_1 + x_2 = x_1^* + x_2^*$ and then travel 'down' the surface on the line $x_1 + x_2 = x_1^* + x_2^*$. Again the direction of travel towards the path depends on the starting point.

Therefore the model described by Equations 3.57 may again be applied to a four variable ecosystem consisting of a omnivore, $x_1$, a dominant omnivore, $x_2$, a herbivore $x_3$, and a plant source, $x_4$. As with Model 3 for the three variable model this model produces a situation where once the combined dominant omnivore and omnivore population size has reached a certain level, $x_1^* + x_2^*$, all four populations have settled down to exist together in equilibrium. Therefore this model produces a similar situation to the previous one but it is both the omnivore populations that determine the equilibrium state of the populations. Time series plots for two different starting points are shown in Figures 3.30 and 3.31. Also shown is a phase plane plot of $x_1$ and $x_2$ which shows the convergence to the line $x_1^* + x_2^*$.

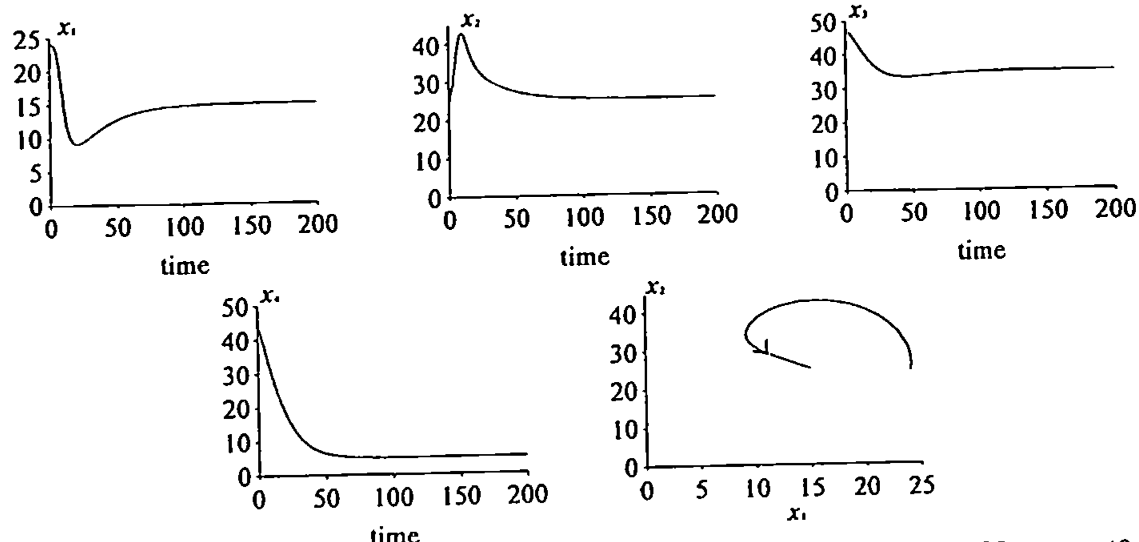

Figure 3.30: Solution curves of Equations 3.57 with $a_1 = 10$, $a_2 = 20$, $a_3 = 30$, $a_4 = 40$, $(x_1^*, x_2^*, x_3^*, x_4^*) = (15, 25, 35, 45)$, $\alpha_1 = 0.01$, $\alpha_2 = 0.02$ and $\alpha_3 = 0.04$ with a starting point of $(24, 24, 48, 45)$

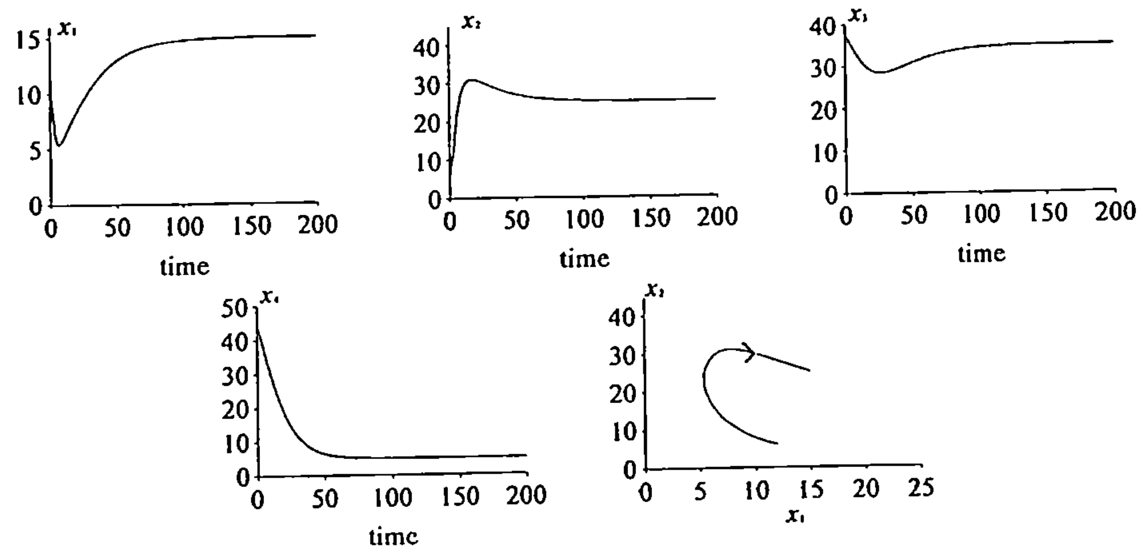

Figure 3.31: Solution curves of Equations 3.57 with $a_1 = 10$, $a_2 = 20$, $a_3 = 30$, $a_4 = 40$, $(x_1^*, x_2^*, x_3^*, x_4^*) = (15, 25, 35, 45)$, $\alpha_1 = 0.01$, $\alpha_2 = 0.02$ and $\alpha_3 = 0.04$ with a starting point of $(12, 6, 37.6, 45)$

## 3.4 Summary

The detailed examination of the two surfaces in this chapter shows that by starting with an easy to visualize surface before trying to expand into higher dimensions provides a good basis for understanding. Even though the differential equation model may look complex, knowing that their solutions traced out a path on the surface of an ellipsoid gave an easy description of their solutions. This in turn made the analysis of the higher dimensional model that much easier.

Once the methodology of creating the model and analysing the behaviour of the path is established it is extremely easy to apply it to higher dimensions. It is always a good learning technique to start with something simple before tackling large complicated models. This method allows this to be done in a very easy way; it is so much easier to understand how the solutions behave if one can actually visualize them.

The six models discussed in this chapter are only a very small subset of those possible. There are many more that could be explored. Attention was paid to these in order for the method of modelling interacting populations via this geometrical approach to be presented. The following chapter examines the same techniques applied to another surface, the torus. This surface is again one that can be easily visualised thus making interpretation easier.

# Chapter 4

# Further geometrical models

## 4.1 A Torus

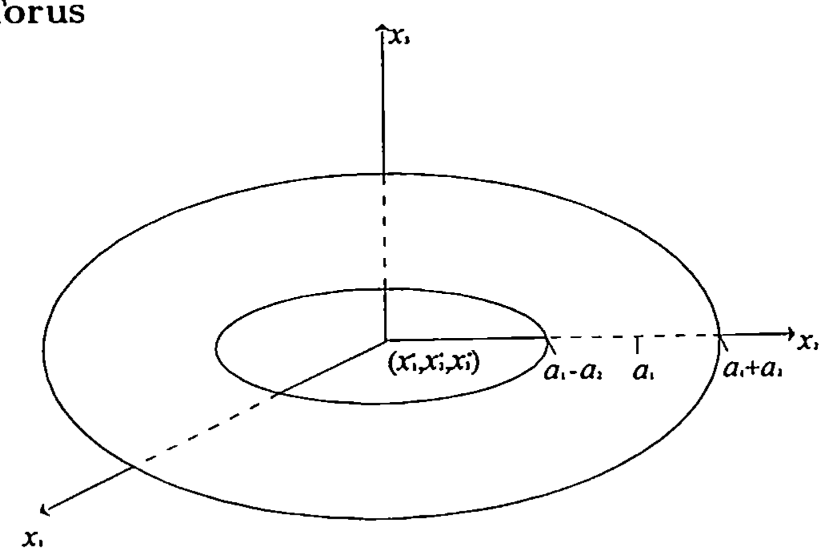


Figure 4.1: Torus, centred at $(x_1^*, x_2^*, x_3^*)$ with characteristic parameters $a_1$ and $a_2$

### 4.1.1 Formulation of the Model

Using a torus leads to a more useful class of models than the ellipsoid discussed in the previous chapter in as much as the $x_3$ component does not necessarily decay with time as it does with the ellipsoid.

The torus shown in Figure 4.1 can be parameterized as follows

$$x_1 - x_1^* = (a_1 + a_2 \sin\theta_2)\cos\theta_1 \tag{4.1a}$$

$$x_2 - x_2^* = (a_1 + a_2 \sin\theta_2)\sin\theta_1 \tag{4.1b}$$

$$x_3 - x_3^* = a_2 \cos\theta_2 \tag{4.1c}$$

To ensure that the torus is entirely within the positive quadrant $x_1^* \geq a_1$, $x_2^* \geq a_1$ and $x_3^* \geq a_2$. To keep the system as general as possible the same principle as with the ellipsoid in the previous chapter is employed and

$$\theta_1 = \alpha_1 f_1(t) + \phi_1 \tag{4.2}$$

$$\theta_2 = \alpha_2 f_2(t) + \phi_2 \tag{4.3}$$

where $\alpha_1$, $\alpha_2$, $\phi_1$ and $\phi_2$ are parameters and $f_1(t)$ and $f_2(t)$ are functions of time $t$. Therefore the general parametric equations of the torus in Figure 4.1 are

$$x_1 - x_1^* = (a_1 + a_2 \sin(\alpha_2 f_2(t) + \phi_2))\cos(\alpha_1 f_1(t) + \phi_1) \tag{4.4a}$$

$$x_2 - x_2^* = (a_1 + a_2 \sin(\alpha_2 f_2(t) + \phi_2))\sin(\alpha_1 f_1(t) + \phi_1) \tag{4.4b}$$

$$x_3 - x_3^* = a_2 \cos(\alpha_2 f_2(t) + \phi_2). \tag{4.4c}$$

To formulate the model, Equations 4.4 are differentiated with respect to time to give

$$\begin{aligned}\frac{\mathrm{d}x_1}{\mathrm{d}t} &= a_2\alpha_2 f_2'(t)\cos(\alpha_2 f_2(t) + \phi_2)\cos(\alpha_1 f_1(t) + \phi_1) \\ &\quad -\alpha_1 f_1'(t)(a_1 + a_2 \sin(\alpha_2 f_2(t) + \phi_2))\sin(\alpha_1 f_1(t) + \phi_1) \qquad (4.5\text{a}) \\ \frac{\mathrm{d}x_2}{\mathrm{d}t} &= a_2\alpha_2 f_2'(t)\cos(\alpha_2 f_2(t) + \phi_2)\sin(\alpha_2 f_1(t) + \phi_1) \\ &\quad +\alpha_1 f_1'(t)(a_1 + a_2 \sin(\alpha_2 f_2(t) + \phi_2))\cos(\alpha_1 f_1(t) + \phi_1) \\ \frac{\mathrm{d}x_3}{\mathrm{d}t} &= -a_2\alpha_2 f_2'(t)\sin(\alpha_2 f_2(t) + \phi_2) \qquad (4.5\text{b})\end{aligned}$$

Using Equations 4.4 expressions for $\sin(\alpha_1 f_1(t) + \phi_1)$, $\cos(\alpha_1 f_1(t) + \phi_1)$, etc. can be found as follows.

$$\begin{aligned}
\sin(\alpha_1 f_1(t) + \phi_1) &= \frac{x_2 - x_2^*}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}} && \text{(4.6a)} \\
\cos(\alpha_1 f_1(t) + \phi_1) &= \frac{x_1 - x_1^*}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}} && \text{(4.6b)} \\
a_1 + a_2 \sin(\alpha_2 f_2(t) + \phi_2) &= \sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} && \text{(4.6c)} \\
\cos(\alpha_2 f_2(t) + \phi_2) &= \frac{x_3 - x_3^*}{a_2} && \text{(4.6d)}
\end{aligned}$$

Using these identities the set of differential equations (Equations 4.5) can be rewritten as

$$\frac{dx_1}{dt} = \frac{\alpha_2 f_2'(t)(x_1 - x_1^*)(x_3 - x_3^*)}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}} - \alpha_1 f_1'(t)(x_2 - x_2^*) \qquad \text{(4.7a)}$$

$$\frac{dx_2}{dt} = \frac{\alpha_2 f_2'(t)(x_2 - x_2^*)(x_3 - x_3^*)}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}} + \alpha_1 f_1'(t)(x_1 - x_1^*) \qquad \text{(4.7b)}$$

$$\frac{dx_3}{dt} = a_1 \alpha_2 f_2'(t) - \alpha_2 f_2'(t)\left(\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}\right) \qquad \text{(4.7c)}$$

Equations 4.7 therefore model a three variable system whose solution curves wander over the surface of a torus whose equation can be written as

$$\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} - a_1 = \sqrt{a_2^2 - (x_3 - x_3^*)^2} \qquad \text{(4.8)}$$

Using similar procedures as in the previous chapter with the ellipsoid, many different models can be formulated from this basic set of equations with different choices for $f_1(t)$ and $f_2(t)$. To get a general idea of how to analyse the solution curves it is beneficial to examine the mathematics of the system.

#### 4.1.1.1 Polar Coordinates

As with the ellipsoid previously, more detail on how the path moves over the surface of the torus can be found by considering the model in a different coordinate system. The torus is easy to represent in cylindrical polar coordinates, $r$ and $\psi$. $r$ is a measure of how far from the centre of the torus, $(x_1^*, x_2^*, x_3^*)$, the solution curve is at any point in time and $\psi$ is a measure of the angle the path makes with the $x_3$ axis. This is illustrated in Figure 4.2.

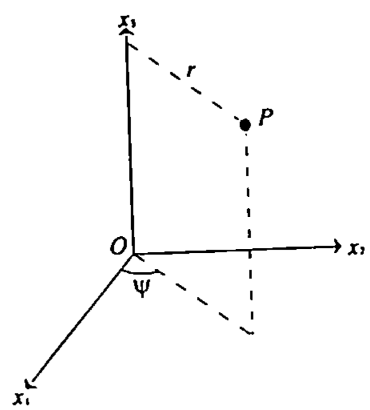


Figure 4.2: Cylindrical polar coordinates

Therefore in cylindrical polar coordinates the system can be represented as

$$x_1 - x_1^* = r\cos\psi \tag{4.9a}$$

$$x_2 - x_2^* = r\sin\psi \tag{4.9b}$$

By comparing these with Equations 4.4 the following expressions are obtained for $r$ and $\psi$.

$$r = a_1 + a_2\sin(\theta_2) = a_1 + a_2\sin(\alpha_2 f_2(t) + \phi_2) \tag{4.10a}$$

$$\psi = \theta_1 = \alpha_1 f_1(t) + \phi_1 \tag{4.10b}$$

This is therefore a similar situation to the ellipsoid in as much that it is the angle $\psi$ which gives an indication whether or not the path circles around the torus. Again $\psi$ is simply a function of $f_1(t)$ and so it will be the choice of $f_1(t)$ which will determine if the path continues to progress around the torus. If however a particular situation called for the path to stop circling i.e. to have constant $x_1$ or $x_2$ then an appropriate choice of $f_1(t)$ should be made so that $\psi$ is no longer an increasing function.

Looking at Equation 4.10a it is obvious that $r$ i.e. the distance the path is from the centre of the torus is such that $a_1 - a_2 \leq r \leq a_1 + a_2$. Now if at any one time the distance of the path from the centre is to be constant i.e. $x_3$ is constant, then from Equation 4.6d, $\cos(\alpha_2 f_2(t) + \phi_2)$ must also be a constant. This implies that $f_2(t)$ equals a constant. If $f_2(t)$ is a constant then the set of differential equations modelling this situation (Equations 4.7) would reduce to two dimensions, i.e. the path would therefore be a circle. Therefore, for the purpose of this thesis, it is necessary to restrict the arbitrary functions, $f_i(t)$, to always be non constant functions of $t$.

Following this restriction, it can be seen that therefore, whatever choice of $f_2(t)$ that is made, the distance the path is from the centre is always fluctuating and so the solution path will continuously 'coil' around the torus.

#### 4.1.1.2 Periodicity

One advantage of this model over that of the ellipsoid based model is that the concept of periodicity can be introduced. The model can be forced to allow the cycle to repeat for a set time period say for example, annually. For the solution to be periodic with period $T$ the following conditions on $x_1$, $x_2$ and $x_3$ need to be imposed:

$$x_1(t^*) = x_1(t^* + T) \tag{4.11}$$

$$x_2(t^*) = x_2(t^* + T) \tag{4.12}$$

$$x_3(t^*) = x_3(t^* + T) \tag{4.13}$$

where $t^*$ is any particular time.

From Equation 4.4c it can be seen that the $x_3$ component is governed by $\cos(\alpha_2 f_2(t) + \phi_2)$. Therefore one of the conditions for a periodic solution is

$$\cos(\alpha_2 f_2(t^*) + \phi_2) = \cos(\alpha_2 f_2(t^* + T) + \phi_2) \tag{4.14}$$

or it is simply sufficient that

$$\alpha_2 f_2(t^*) + \phi_2 = \alpha_2 f_2(t^* + T) + \phi_2 \pm 2\pi m_1 \tag{4.15}$$

where $m_1 = 0, 1, 2, \ldots$.

If Equation 4.15 is satisfied then it is also required that

$$\sin(\alpha_1 f_1(t^*) + \phi_1) = \sin(\alpha_1 f_1(t^* + T) + \phi_1) \tag{4.16a}$$

$$\cos(\alpha_1 f_1(t^*) + \phi_1) = \cos(\alpha_1 f_1(t^* + T) + \phi_1) \tag{4.16b}$$

Again it is sufficient that

$$\alpha_1 f_1(t^*) + \phi_1 = \alpha_1 f_1(t^* + T) + \phi_1 \pm 2\pi m_2 \tag{4.17}$$

where $m_2 = 0, 1, 2, \ldots$.

It is the values of $\alpha_1$ and $\alpha_2$ which controls the position of the path at any time $t$. For known periods it should therefore be possible to find values for $\alpha_1$ and $\alpha_2$ for which Equations 4.15 and 4.17 are valid. Subsequently if the model is required to behave in such a cyclic nature then the only free parameters are $a_1$ and $a_2$ i.e. those that define the 'shape' of the torus.

Looking at the equations that define the model it can be seen that the parameter $a_2$ does not appear in them. This means that the surface of the torus is not defined until the boundary conditions (that is, the start values) are given. On defining the starting point the shape of the torus is defined. If Equations 4.7 are solved for any starting point then the solutions will always lie on a torus whose characteristic parameters could be obtained.

### 4.1.2 Many Models From One

In this section choices of $f_1'(t)$ and $f_2'(t)$ are made to build a collection of different models. As with the ellipsoid one aim of this approach is to simplify the models and similar to the algebra in Section 3.2.2 the square root term can be simplified by letting

$$f_2'(t) = f_3(t)\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} \tag{4.18}$$

where $f_3(t)$ is a function of time $t$. The three differential equations and hence the basic model are

$$\begin{aligned}
\frac{\mathrm{d}x_1}{\mathrm{d}t} &= \alpha_2 f_3(t)(x_1 - x_1^*)(x_3 - x_3^*) - \alpha_1 f_1'(t)(x_2 - x_2^*) && \text{(4.19a)}\\
\frac{\mathrm{d}x_2}{\mathrm{d}t} &= \alpha_2 f_3(t)(x_2 - x_2^*)(x_3 - x_3^*) + \alpha_1 f_1'(t)(x_1 - x_1^*) && \text{(4.19b)}\\
\frac{\mathrm{d}x_3}{\mathrm{d}t} &= a_1\alpha_2 f_3(t)\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} - \alpha_2 f_3(t)((x_1 - x_1^*)^2 + (x_2 - x_2^*)^2) && \text{(4.19c)}
\end{aligned}$$

#### 4.1.2.1 Model 1

Here the choices for $f_1'(t)$ and $f_3(t)$ are those which lead to a simple model for the three variables. A choice of

$$\begin{aligned}
f_1'(t) &= 1 && \text{(4.20)}\\
f_3(t) &= 1 && \text{(4.21)}
\end{aligned}$$

produce the following set of differential equations and hence the model.

$$\frac{dx_1}{dt} = \alpha_2(x_1 - x_1^*)(x_3 - x_3^*) - \alpha_1(x_2 - x_2^*) \tag{4.22a}$$

$$\frac{dx_2}{dt} = \alpha_2(x_2 - x_2^*)(x_3 - x_3^*) + \alpha_1(x_1 - x_1^*) \tag{4.22b}$$

$$\frac{dx_3}{dt} = a_1\alpha_2\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} - \alpha_2((x_1 - x_1^*)^2 + (x_2 - x_2^*)^2) \tag{4.22c}$$

With the ellipsoid a major help to finding how the solution curve behaved was to examine the fixed points and stability of the system. In this model however the analysis is not so straightforward. The fixed points of the system occur when the derivatives in Equations 4.22 equal zero. It can be seen that this occurs when $x_1 = x_1^*$ and $x_2 = x_2^*$. However $x_3$ can be any arbitrary value. This implies that this set of equations do not possess a unique fixed point but, in effect, a fixed *line*. This line does not sit on the torus but runs through the middle of it. It is possible that this line behaves in the manner of a centre with neutral stability as described in Section 2.3.2 on page 23

However the Jacobian matrix for this system is given by

$$\mathbf{J} = \begin{bmatrix} \alpha_2(x_3 - x_3^*) & -\alpha_1 & \alpha_2(x_1 - x_1^*) \\ \alpha_1 & \alpha_2(x_3 - x_3^*) & \alpha_2(x_2 - x_2^*) \\ \frac{\alpha_2(x_1 - x_1^*)^2\left(a_1 - 2\sqrt{(x_1 - x_1^*) + (x_2 - x_2^*)}\right)}{\sqrt{(x_1 - x_1^*) + (x_2 - x_2^*)}} & \frac{\alpha_2(x_2 - x_2^*)^2\left(a_1 - 2\sqrt{(x_1 - x_1^*) + (x_2 - x_2^*)}\right)}{\sqrt{(x_1 - x_1^*) + (x_2 - x_2^*)}} & 0 \end{bmatrix} \tag{4.23}$$

and when this is evaluated for $x_1 = x_1^*$ and $x_2 = x_2^*$ the matrix cannot be defined due to the division by zero. Therefore the nature of the stability of this system cannot be determined in this way.

Nevertheless, it is still possible to see how the solution to Equations 4.22 behaves by examination of $\psi$ for this choice of $f_1'(t)$. On integration Equation 4.20 becomes

$$f_1(t) = t + k_2 \tag{4.24}$$

where $k_2$ is the constant of integration. Hence Equation 4.10b is in this case

$$\psi = \alpha_1(t + k_2) + \phi_1 \tag{4.25}$$

and it is obvious that as $t$ increases then $\psi$ also increases and so the solution curve will travel in an anticlockwise direction around the torus.

As discussed on page 90, it is the function $\theta_2$ which determines the 'coiling' of the path around the torus. It was found that $f_2(t)$ can be any function of $t$ whatsoever and the path will always coil around the torus. This can be confirmed by examining the choice of $f_2(t)$ for this model.

$$f_2'(t) = \sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} \tag{4.26}$$

which integrates to give

$$\theta_2 = \alpha_2 f_2(t) + \phi_2 = 2\tan^{-1}\Big[\frac{\sqrt{a_1^2 - a_2^2}}{a_1}\tan[\frac{1}{2}\alpha_2\sqrt{a_1^2 - a_2^2}(t + k_1)] - a_2\Big] \tag{4.27}$$

(More details of this integration are shown in Appendix B.) Now since $t$ is increasing at a constant rate, $\theta_2$ will never be constant, it fluctuates between $\pm\pi$ and hence $\sin\theta_2$ will fluctuate between $\pm 1$. Therefore the distance of the path from the centre of the torus will always be fluctuating between $a_1 \pm a_2$ and hence the path will always be coiling around the torus. A typical path for this model is shown in Figure 4.3.

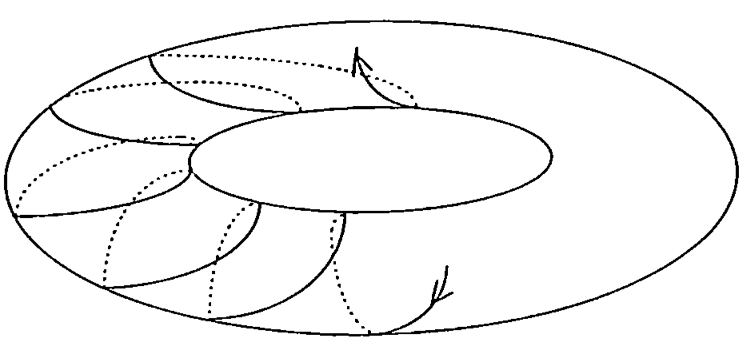


Figure 4.3: A typical solution curve of Equations 4.22

Looking at Equations 4.22 it can be seen that they can be representative of a three variable ecosystem that consists of a herbivore, $x_1$, an omnivore, $x_2$, and a plant source, $x_3$. The herbivore utilise the plant source who are in turn consumed by the omnivore. The omnivore population grows due to eating the herbivore and also by the consumption of the plant source. By examining equation 4.22c it can be seen that there are two competing mechanisms, one depleting the plant source and the other replenishing it. This could be interpreted as regeneration of the plant source due to the presence of the other two species i.e. pollination, seed dispersal or fertilisation increasing the growth rate.

In terms of the three species it means that none of them will ever die out. When the plant source is plentiful the herbivore and omnivore both have enough to eat and so are also plentiful. Now the plant source will begin to die away since they are being consumed faster than they are being replenished. This however causes a fall in the numbers of herbivores and omnivores since they both now have less to eat. The omnivore population size will fall after the herbivore population since it has the alternative food source i.e. the herbivore. The fall in the numbers of these two causes the plant source to build up once more and the cycle starts again.

If it is required for the cycle to be periodic i.e. repeat over a set time period, as discussed in Section 4.1.1.2 then the choices for $f_1'(t)$ and $f_2'(t)$ need to be examined in further detail in order that expressions for $\alpha_2$ and $\alpha_1$ can be found.

For this model the choice of $f_2'(t)$ was made to be

$$
\begin{aligned}
f_2'(t) &= \sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} && (4.28)\\
&= a_1 + a_2 \sin(\alpha_2 f_2(t) + \phi_2) && (4.29)
\end{aligned}
$$

and so

$$
\alpha_2 f_2(t) + \phi_2 = 2\tan^{-1}\Big[\frac{\sqrt{a_1^2 - a_2^2}}{a_1}\tan\big(\frac{1}{2}\alpha_2\sqrt{a_1^2 - a_2^2}(t + k_1)\big) - a_2\Big] \qquad (4.30)
$$

where $k_1$ is the constant of integration. Therefore to satisfy Equation 4.15 so that the cycle is periodic with period $T$, it is sufficient to allow

$$\frac{1}{2}\alpha_2\sqrt{a_1^2 - a_2^2}(t^* + k_1) = \frac{1}{2}\alpha_2\sqrt{a_1^2 - a_2^2}(t^* + T + k_1) \pm 2\pi m_1 \tag{4.31}$$

or simply that

$$\alpha_2 = \frac{4\pi m_1}{T\sqrt{a_1^2 - a_2^2}} \tag{4.32}$$

where $m_1 = 1, 2 \ldots$. Thus, for a known period, the value of $\alpha_2$ to produce such a cycle can easily be determined.

A similar argument now needs to be followed to produce an expression for $\alpha_1$. For this model the choice for $f_1(t)$ was such that

$$f_1(t) = t + k_2. \tag{4.33}$$

Therefore for Equation 4.17 to be satisfied it is sufficient to require

$$\alpha_1(t^* + k_2) + \phi_1 = \alpha_1(t^* + T + k_2) + \phi_1 \pm 2\pi m_2 \tag{4.34}$$

and similarly an expression for $\alpha_1$ is obtained in terms of the period $T$ i.e.

$$\alpha_1 = \frac{2\pi m_2}{T} \tag{4.35}$$

where $m_2 = 1, 2, \ldots$

In terms of the path on the surface the value of $\alpha_2$ determines how many 'coils' there are around the torus. The integer $m_1$ in Equation 4.32 allows the size of $\alpha_2$ to be varied to fit each situation. Doubling of $m_1$ allows twice as many 'coils' around the torus over the same time, tripling it invokes three times as many. The parameter $\alpha_1$ affects the rate of decay of $x_1$ due to the interaction with $x_2$. and it value determines how many 'circuits' of the torus there are over the given period. With $m_2 = 1$ then the path will travel one circuit of the torus in the period $T$. Increasing $m_2$ to 2 has the effect of halving the period i.e. causing the path to travel twice around the torus in the period. A combination of different $m_1$'s and $m_2$'s has the effect of combining their attributes. For example with $m_1 = 3$ and $m_2 = 2$ the number of coils around the torus is tripled but over twice a long a time and therefore having the effect of one and half as many coils on one circuit.

Time series plots for different values of $m_1$ are shown in figures 4.4 to 4.6. The effect of changing the value of $m_2$ is shown in Figure 4.7. The period is chosen to be 1 year i.e. 365 days. The phase plane plot of $x_1$ against $x_2$ is shown in each case to show the path around the torus. Changing the 'shape' of the torus has the effect of altering the size of the small fluctuations within the main cycle. A 'fat' torus i.e. with $a_2$ of a value close to $a_1$ will thus produce larger fluctuations than a 'thin' torus i.e. one with $a_2$ of a value much smaller than $a_1$. Figures 4.8 and 4.9 show the solution curves on two such tori.

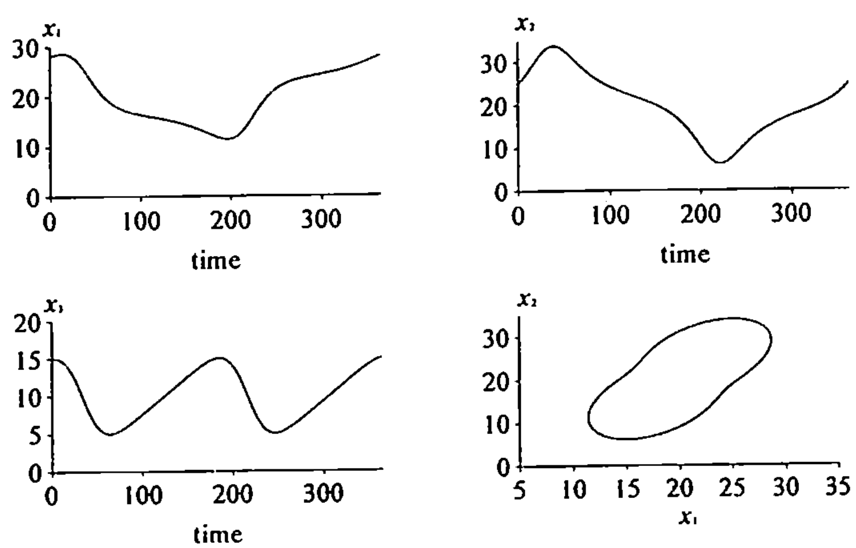


Figure 4.4: Solution curves of Equations 4.22 with $m_1 = 1$, $m_2 = 1$, $a_1 = 10$, $a_2 = 5$ and $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$.

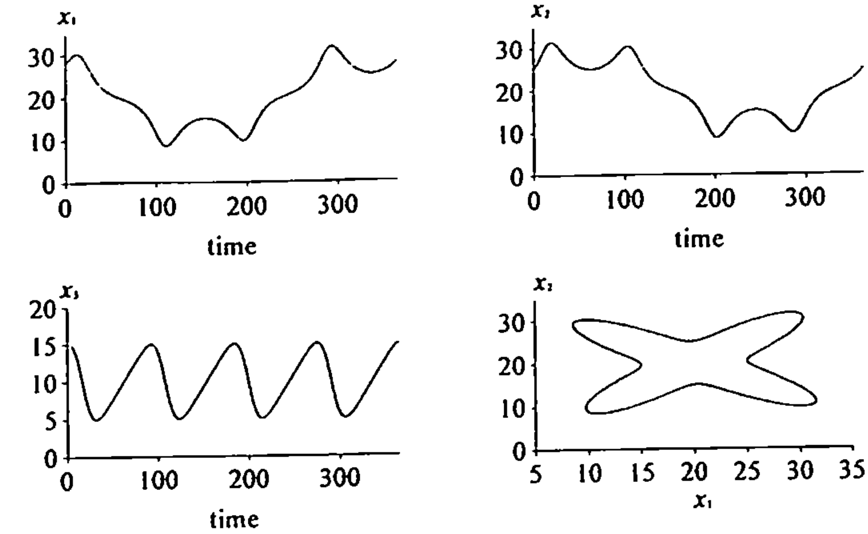


Figure 4.5: Solution curves of Equations 4.22 with $m_1 = 2$, $m_2 = 1$, $a_1 = 10$, $a_2 = 5$ and $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$.

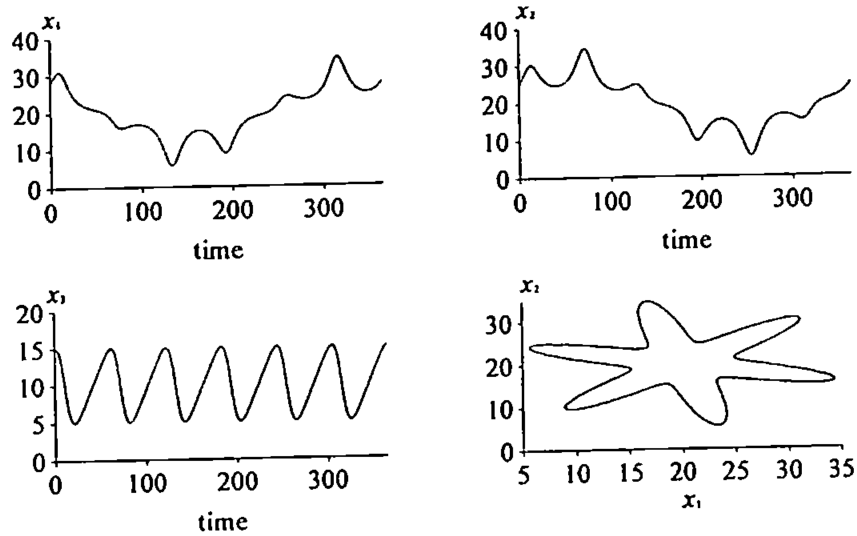


Figure 4.6: Solution curves of Equations 4.22 with $m_1 = 3$, $m_2 = 1$, $a_1 = 10$, $a_2 = 5$ and $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$.

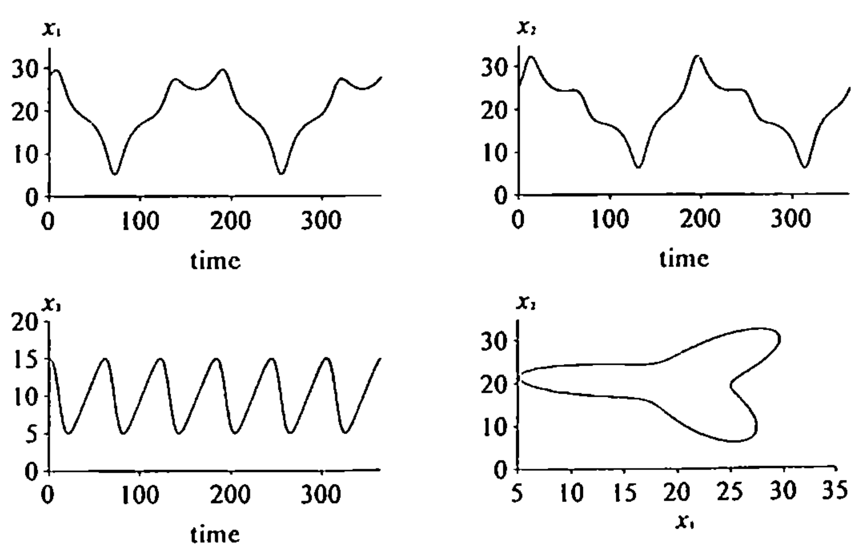


Figure 4.7: Solution curves of Equations 4.22 with $m_1 = 2$, $m_2 = 2$, $a_1 = 10$, $a_2 = 5$ and $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$.

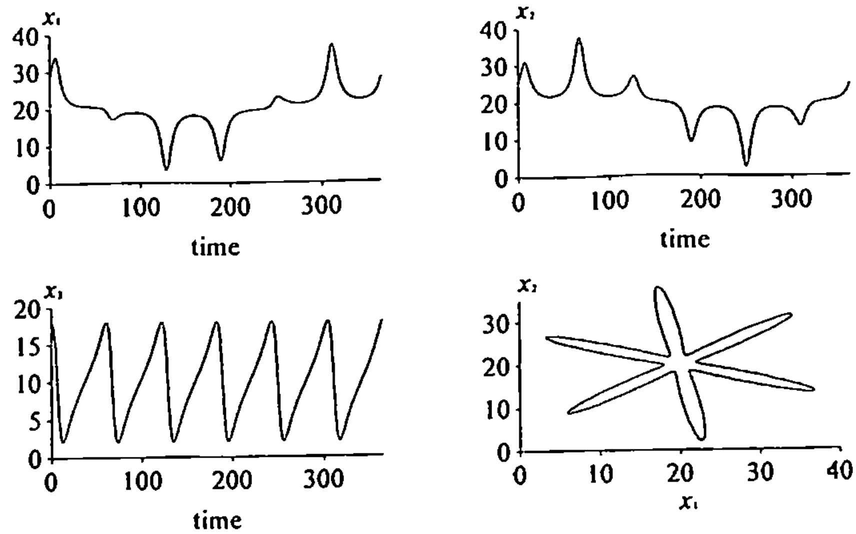


Figure 4.8: Solution curves of Equations 4.22 with $m_1 = 3$, $m_2 = 1$, $a_1 = 10$ $a_2 = 8$ and $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$.

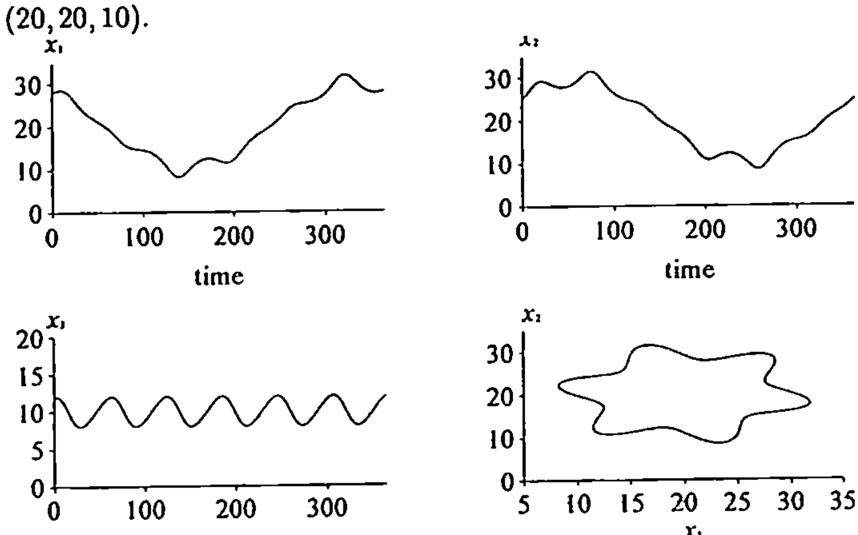


Figure 4.9: Solution curves of Equations 4.22 with $m_1 = 3$, $m_2 = 1$, $a_1 = 10$, $a_2 = 8$ and $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$.

### 4.1.2.2 Model 2

To incorporate an $x_1x_2$ term into the second term of the right hand sides of Equations 4.7a and b the choice of $f_1(t)$ is made such that

$$f_1'(t) = (x_1 - x_1^*)(x_2 - x_2^*) \tag{4.36}$$

and for simplicity

$$f_3(t) = 1 \tag{4.37}$$

The differential equations for such a model are therefore

$$
\begin{aligned}
\frac{\mathrm{d}x_1}{\mathrm{d}t} &= \alpha_2(x_1 - x_1^*)(x_3 - x_3^*) - \alpha_1(x_2 - x_2^*)^2(x_1 - x_1^*) && (4.38a)\\
\frac{\mathrm{d}x_2}{\mathrm{d}t} &= \alpha_2(x_2 - x_2^*)(x_3 - x_3^*) + \alpha_1(x_1 - x_1^*)^2(x_2 - x_2^*) && (4.38b)\\
\frac{\mathrm{d}x_3}{\mathrm{d}t} &= a_1\alpha_2(\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}) - \alpha_2((x_1 - x_1^*)^2 + (x_2 - x_2^*)^2) && (4.38c)
\end{aligned}
$$

To analyse the path of the solution curves to Equations 4.38 examination of $\psi$ and therefore $f_1(t)$ is required.

$$\frac{\mathrm{d}f_1(t)}{\mathrm{d}t} = (a + b\sin(\alpha_2 f_2(t) + \phi_2))^2 \cos(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_1 f_1(t) + \phi_1) \qquad (4.39)$$

from Equations 4.4 and so

$$\int \frac{\mathrm{d}f_1(t)}{\cos(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_1 f_1(t) + \phi_1)} = \int (a + b\sin(\alpha_2 f_2(t) + \phi_2))^2 \mathrm{d}t \qquad (4.40)$$

This integrates to

$$\alpha_1 f_1(t) + \phi_1 = \tan^{-1}(2\mathrm{e}^{\frac{\alpha_1}{\alpha_2}(a_1(\alpha_2 f_2(t)+\phi_2) - a_2\cos(\alpha_2 f_2(t)+\phi_2)}) \qquad (4.41)$$

where $\alpha_2 f_2(t) + \phi_2 = 2\tan^{-1}\left[\frac{\sqrt{a_1^2 - a_2^2}}{a_1}\tan[\frac{1}{2}\alpha_2\sqrt{a_1^2 - a_2^2}(t + k_1)] - a_2\right]$.

This is very similar to the analysis in Model 2 of the three–dimensional ellipsoid on page 61 in that $\psi$ will lie in the range $0 \le \psi \le \pi/2$ and so the path will not move further than 90° from the $x_1$ axis. By looking at $\frac{\mathrm{d}\psi}{\mathrm{d}t}$ it can be seen that

$$
\begin{aligned}
\frac{\mathrm{d}\psi}{\mathrm{d}t} &= \alpha_1 f_1'(t) && (4.42)\\
&= \alpha_1(x_1 - x_1^*)(x_2 - x_2^*) && (4.43)
\end{aligned}
$$

and so when the path reaches such a point that either $x_1 = x_1^*$ or $x_2 = x_2^*$ then $\psi$ is constant and the path stops revolving around the torus. Following a similar argument to that for the ellipsoid the path will always travel towards $x_1^*$ rather than $x_2^*$. Whether the movement is in a clockwise or anticlockwise direction will depend on the starting point. Considering an $x_1x_2$ plane view of the torus as shown in Figure 4.10 the starting point can be in any of the four quadrants.

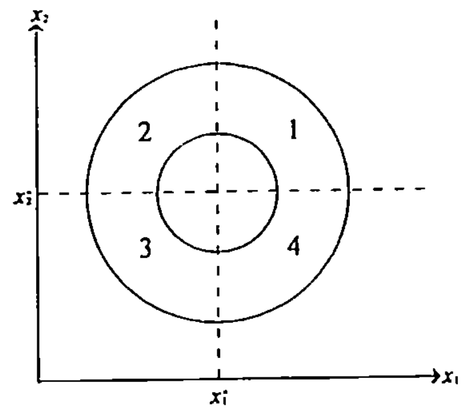


Figure 4.10: $x_1x_2$ plane view of the torus at $x_3 = x_3^*$

If the starting point is in quadrants 1 or 3 then the path will move in an anticlockwise direction towards the line $x_1 = x_1^*$ since $\frac{d\psi}{dt}$ will be positive. If the starting point is in quadrants 2 or 4 then the path will move in an clockwise direction towards the line $x_1 = x_1^*$ since $\frac{d\psi}{dt}$ will be negative. Once $x_1 = x_1^*$ there will be no further movement in the $x_1$ direction but the path will continue to coil around the torus in that plane. A typical path is shown in Figure 4.11 overleaf.

Again, this model can represent a herbivore, $x_1$, an omnivore, $x_2$, and plant source, $x_3$. However in this case, once the herbivore, $x_1$, has reached a certain level, $x_1^*$, it maintains that level. The natural growth rate is matched by its death rate due to the predation by the omnivore, $x_2$. The omnivore and the plant source continue to fluctuate continuously as the plant source gets depleted, the omnivore population decreases, the plant source is allowed to regenerate thus allowing the omnivore population to increase again.

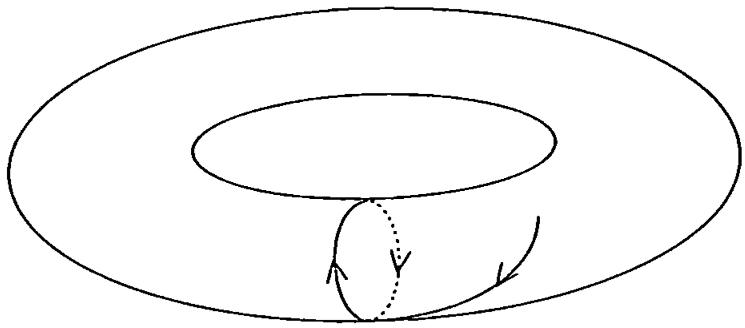

Figure 4.11: A typical solution curve of Equations 4.38

Time series plots for the solutions of Equations 4.38 are shown in Figures 4.12 to 4.15 for four different starting points. The phase plot for $x_1 x_2$ is shown to illustrate the convergence to the point $x_1^*$.

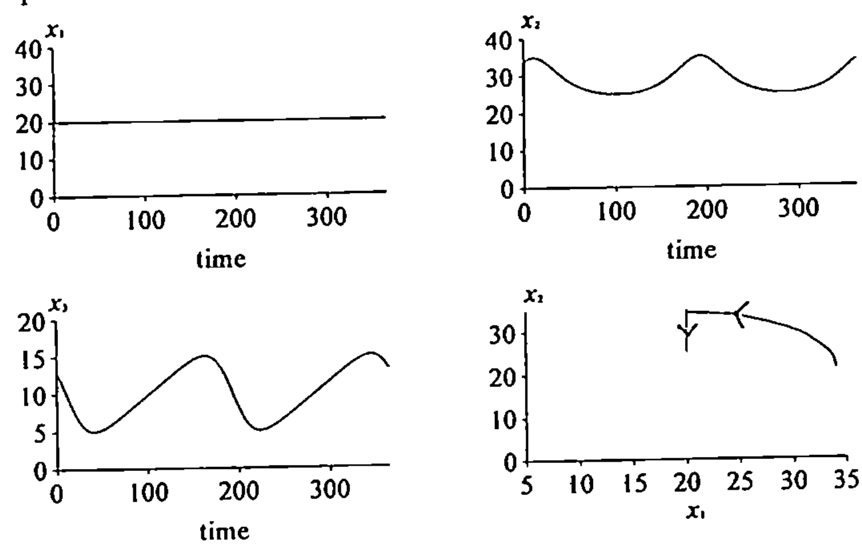


Figure 4.12: Solution curves of Equations 4.38 with $m_1 = 1$, $m_2 = 1$, $a_1 = 10$ $a_2 = 5$, $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$ with a starting point of $(34, 21, 12.95)$

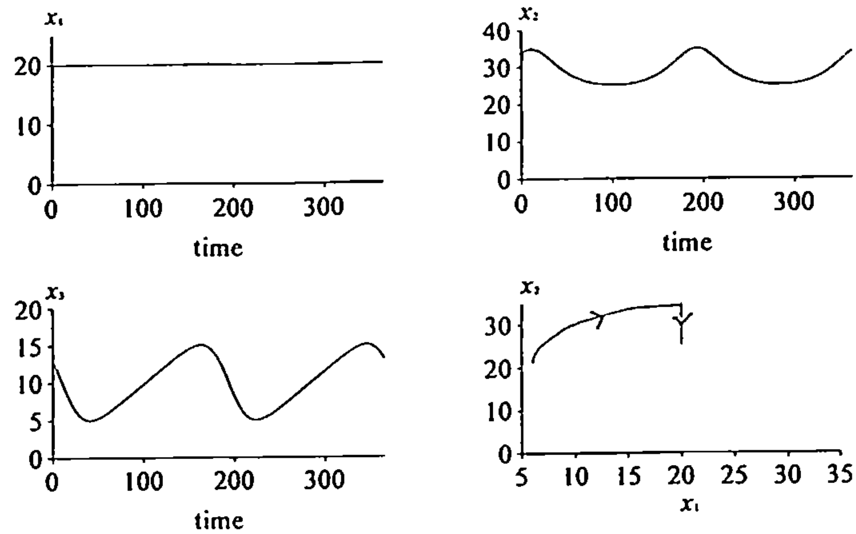

Figure 4.13: Solution curves of Equations 4.38 with $m_1 = 2$, $m_2 = 2$, $a_1 = 10$, $a_2 = 5$ and $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$ with a starting point of $(6, 21, 12.95)$

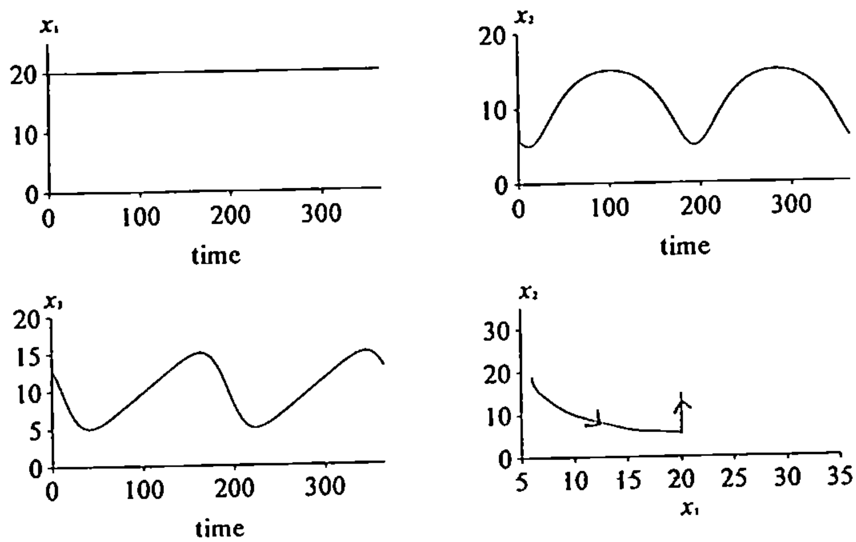

Figure 4.14: Solution curves of Equations 4.38 with $m_1 = 3$, $m_2 = 1$, $a_1 = 10$ $a_2 = 8$ and $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$ with a starting point of $(6, 19, 12.95)$

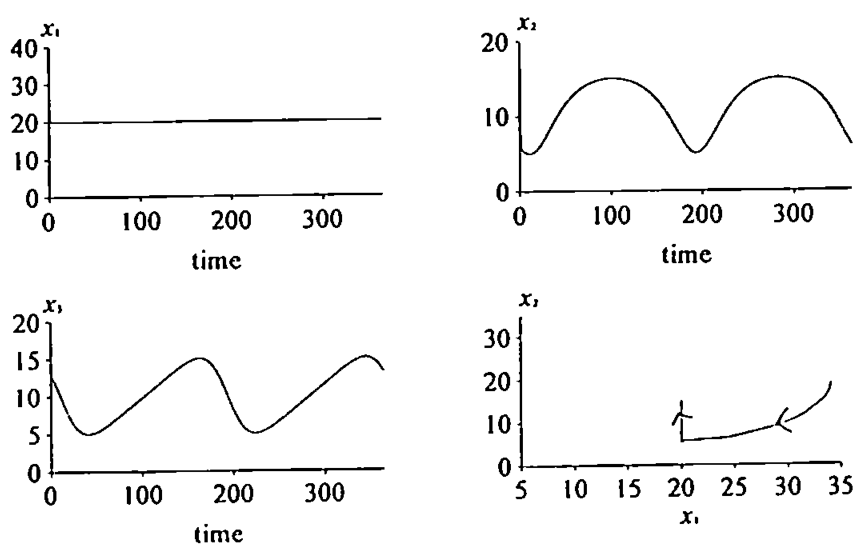

Figure 4.15: Solution curves of Equations 4.38 with $m_1 = 3$, $m_2 = 1$, $a_1 = 10$ $a_2 = 8$ and $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$ with a starting point of $(34, 19, 12.95)$

#### 4.1.2.3 Model 3

A further choice of $f_1'(t)$ which produces an $x_1x_2$ term in the $x_1$ and $x_2$ equations of the general model is

$$f_1'(t) = (x_1 - x_1^*) + (x_2 - x_2^*) \tag{4.44}$$

With $f_3(t)$ remaining equal to 1 the differential equations forming this model are

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = \alpha_2(x_1 - x_1^*)(x_3 - x_3^*) - \alpha_1(x_1 - x_1^*)(x_2 - x_2^*) - \alpha_1(x_2 - x_2^*)^2 \tag{4.45a}$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = \alpha_2(x_2 - x_2^*)(x_3 - x_3^*) + \alpha_1(x_1 - x_1^*)(x_2 - x_2^*) + \alpha_1(x_1 - x_1^*)^2 \tag{4.45b}$$

$$\frac{\mathrm{d}x_3}{\mathrm{d}t} = a_1\alpha_2(\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}) - \alpha_2((x_1 - x_1^*)^2 + (x_2 - x_2^*)^2) \tag{4.45c}$$

Following on from the analysis performed on the behaviour of the path in Model 2 and noting its similarity with the analysis in the previous chapter, the behaviour of the solution curves for *this* model can be predicted. It would be expected that the path moves around the torus until it reaches the plane $x_1 + x_2 = x_1^* + x_2^*$. The path will then cease circling the torus but continue to coil around it where the torus cuts the plane. This will be a slightly more interesting outcome than that of Model 2 considered previously because both $x_1$ and $x_2$ will continue to fluctuate. Again the starting point will determine the direction of travel. Consider an $x_1x_2$ plane view of the torus as shown in Figure 4.16 below.

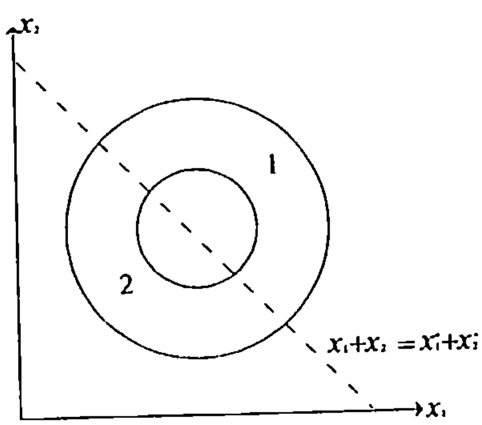


Figure 4.16: $x_1x_2$ plane view of the torus at $x_3 = x_3^*$

If the starting point is such that $x_1 + x_2 > x_1^* + x_2^*$ i.e. in section 1 of Figure 4.16 then $\frac{d\psi}{dt} > 0$ and the path will move in an anticlockwise direction around the torus. If the starting point is such that $x_1 + x_2 < x_1^* + x_2^*$ i.e. in section 2 of Figure 4.16 then $\frac{d\psi}{dt} < 0$ and the path will move in an clockwise direction around the torus. A typical path is shown in Figure 4.17.

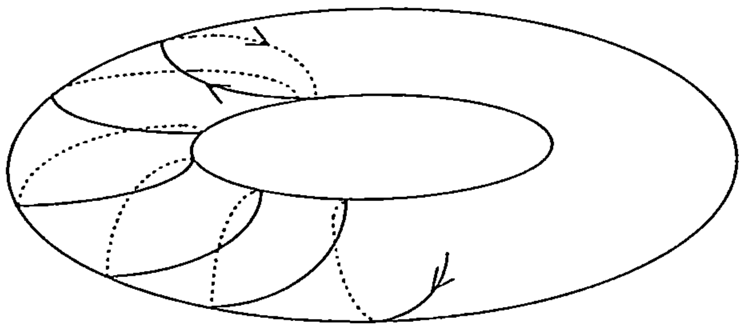

Figure 4.17: A typical solution curve of Equations 4.45

Again this model produces a similar situation to that for previous model. Equations 4.45 can again be interpreted in terms of an ecosystem consisting of three species $x_1$, $x_2$ and $x_3$, a herbivore, an omnivore and a plant source respectively. This model produces a situation where once the combined herbivore and omnivore population size has reached a certain level, $x_1^* + x_2^*$, they fluctuate around that level. This is very similar to the Lotka–Volterra predator prey model but in three dimensions. The fluctuations are caused by the interaction of the three species, when the omnivore is plentiful, the herbivore population decreases, this allows the plant source to increase. The decrease in the herbivore population size causes the omnivore population to decrease, the herbivore population increases again, the plant source decreases, the omnivore population increases, and the cycle starts over again. Therefore this model produces situation that is maybe more realistic than the previous one since all three members of the ecosystem are constantly interacting with each other.

Time series plots for the solutions of Equations 4.45 are shown in Figures 4.18 to 4.19 for two different starting points.

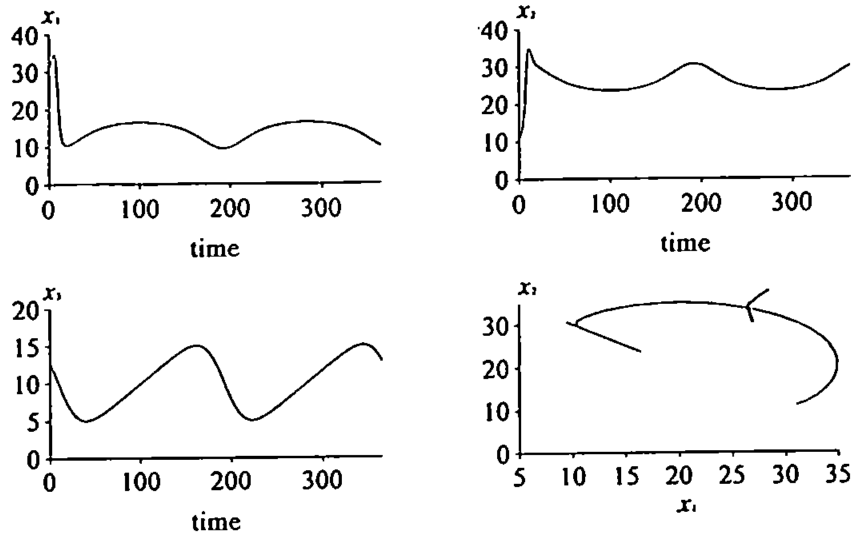


Figure 4.18: Solution curves of Equations 4.45 with $m_1 = 1$, $m_2 = 1$, $a_1 = 10$, $a_2 = 5$, $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$ with a starting point of $(31, 11, 12.69)$

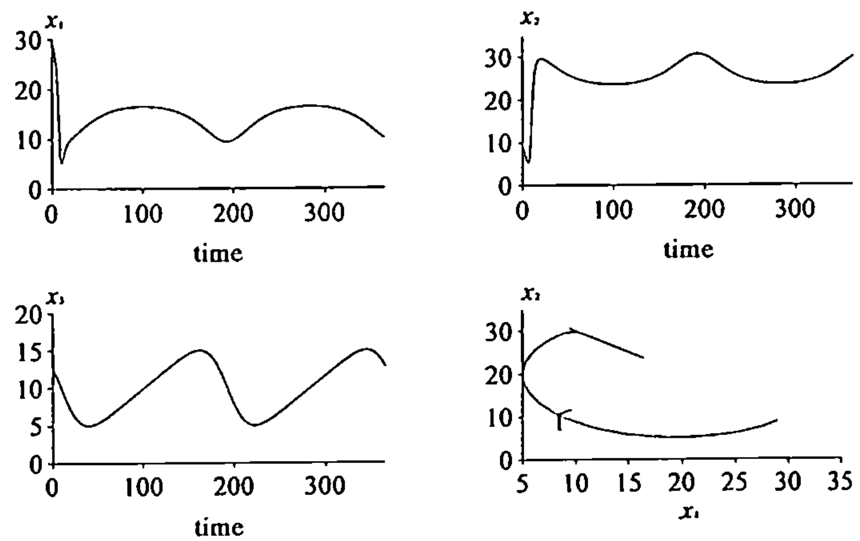


Figure 4.19: Solution curves of Equations 4.45 with $m_1 = 1$, $m_2 = 1$, $a_1 = 10$, $a_2 = 5$, $(x_1^*, x_2^*, x_3^*) = (20, 20, 10)$ with a starting point of $(29, 9, 12.69)$

### 4.1.3 Summary

It can be seen that the formulation of the models in this section on the torus follow a similar pattern to that discussed previously in Chapter 3. The three models that are discussed are only a small sample of different ones which can be formulated from the basic model with further choices of $f_1'(t)$ and $f_3(t)$. However by examining them in some detail and by using a three-dimensional surface that can easily be visualised the procedures can be once again extended to spaces of higher dimensions. In the following section the analysis is extended to four variables and a four dimensional 'torus' is considered.

## 4.2 Four–dimensional 'Torus'

The extension of the basic torus model to four-dimensions can be made by examining the changes in the parametric equations for the ellipsoid (Equations 3.2) and those for the four-dimensional ellipsoid (Equations 3.39) and then applying similar changes to the parametric equations for the torus (Equations 4.1). Thus a set of parametric equations for a four-dimensional torus are

$$x_1 - x_1^* = (a_1 + a_2 \sin\theta_3)\sin\theta_2\cos\theta_1 \tag{4.46a}$$

$$x_2 - x_2^* = (a_1 + a_2 \sin\theta_3)\sin\theta_2\sin\theta_1 \tag{4.46b}$$

$$x_3 - x_3^* = (a_1 + a_2 \sin\theta_3)\cos\theta_2 \tag{4.46c}$$

$$x_4 - x_4^* = a_2\cos\theta_3 \tag{4.46d}$$

A general set of parametric equations can be formulated by allowing

$$\theta_1 = \alpha_1 f_1(t) + \phi_1 \tag{4.47}$$

$$\theta_2 = \alpha_2 f_2(t) + \phi_2 \tag{4.48}$$

$$\theta_3 = \alpha_3 f_3(t) + \phi_3 \tag{4.49}$$

where $\alpha_1$, $\alpha_2$, $\alpha_3$, $\phi_1$, $\phi_2$ and $\phi_3$ are parameters and $f_1(t)$, $f_2(t)$ and $f_2(t)$ are functions of time $t$. Therefore the general parametric equations for a curve drawn on this four dimensional torus are

$$x_1 - x_1^* = (a_1 + a_2\sin(\alpha_3 f_3(t) + \phi_3))\sin(\alpha_2 f_2(t) + \phi_2)\cos(\alpha_1 f_1(t) + \phi_1) \tag{4.50a}$$

$$x_2 - x_2^* = (a_1 + a_2\sin(\alpha_3 f_3(t) + \phi_3))\sin(\alpha_2 f_2(t) + \phi_2)\sin(\alpha_1 f_1(t) + \phi_1) \tag{4.50b}$$

$$x_3 - x_3^* = (a_1 + a_2\sin(\alpha_3 f_3(t) + \phi_3))\cos(\alpha_2 f_2(t) + \phi_2) \tag{4.50c}$$

$$x_4 - x_4^* = a_2\cos(\alpha_3 f_3(t) + \phi_3) \tag{4.50d}$$

Differentiating Equations 4.50 with respect to $t$ to form the basis for the model the following set of equations is formed.

$$\begin{aligned}
\frac{\mathrm{d}x_1}{\mathrm{d}t} &= a_2\alpha_3 f_3'(t)\cos(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_2 f_2(t) + \phi_2)\cos(\alpha_3 f_3(t) + \phi_3) \\
&\quad + \alpha_2 f_2'(t)(a_1 + a_2\sin(\alpha_3 f_3(t) + \phi_3))\cos(\alpha_1 f_1(t) + \phi_1)\cos(\alpha_2 f_2(t) + \phi_2) \\
&\quad - \alpha_1 f_1'(t)(a_1 + a_2\sin(\alpha_3 f_3(t) + \phi_3))\sin(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_2 f_2(t) + \phi_2) \qquad (4.51a) \\
\frac{\mathrm{d}x_2}{\mathrm{d}t} &= a_2\alpha_3 f_3'(t)\sin(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_2 f_2(t) + \phi_2)\cos(\alpha_3 f_3(t) + \phi_3) \\
&\quad + \alpha_2 f_2'(t)(a_1 + a_2\sin(\alpha_3 f_3(t) + \phi_3))\sin(\alpha_1 f_1(t) + \phi_1)\cos(\alpha_2 f_2(t) + \phi_2) \\
&\quad + \alpha_1 f_1'(t)(a_1 + a_2\sin(\alpha_3 f_3(t) + \phi_3))\cos(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_2 f_2(t) + \phi_2) \qquad (4.51b) \\
\frac{\mathrm{d}x_3}{\mathrm{d}t} &= a_2\alpha_3 f_3'(t)\cos(\alpha_2 f_2(t) + \phi_2)\cos(\alpha_3 f_3(t) + \phi_3) \\
&\quad - \alpha_2 f_2'(t)(a_1 + a_2\sin(\alpha_3 f_3(t) + \phi_3))\sin(\alpha_2 f_2(t) + \phi_2) \qquad (4.51c) \\
\frac{\mathrm{d}x_4}{\mathrm{d}t} &= -a_2\alpha_3 f_3'(t)\sin(\alpha_3 f_3(t) + \phi_3) \qquad (4.51d)
\end{aligned}$$

Using Equations 4.50 expressions for $\sin(\alpha_1 f_1(t) + \phi_1)$, $\cos(\alpha_1 f_1(t) + \phi_1)$, etc. can be found. The similarities between these and those for the four dimensional ellipsoid (Equations 3.42) is obvious.

$$\sin(\alpha_1 f_1(t) + \phi_1) = \frac{x_2 - x_2^*}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}} \tag{4.52a}$$

$$\cos(\alpha_1 f_1(t) + \phi_1) = \frac{x_1 - x_1^*}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}} \tag{4.52b}$$

$$\sin(\alpha_2 f_2(t) + \phi_2) = \frac{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2}} \tag{4.52c}$$

$$\cos(\alpha_2 f_2(t) + \phi_2) = \frac{x_3 - x_3^*}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2}} \quad (4.52d)$$

$$a_1 + a_2 \sin(\alpha_3 f_3(t) + \phi_3) = \sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2} \quad (4.52e)$$

$$\cos(\alpha_3 f_3(t) + \phi_3) = \frac{x_4 - x_4^*}{a_2} \quad (4.52f)$$

Using these identities the set of differential equations (Equations 4.51) can be rewritten as

$$\frac{dx_1}{dt} = \frac{\alpha_2 f_2'(t)(x_1 - x_1^*)(x_3 - x_3^*)}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}} + \frac{\alpha_3 f_3'(t)(x_1 - x_1^*)(x_4 - x_4^*)}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2}}$$
$$-\alpha_1 f_1'(t)(x_2 - x_2^*) \quad (4.53a)$$

$$\frac{dx_2}{dt} = \frac{\alpha_2 f_2'(t)(x_2 - x_2^*)(x_3 - x_3^*)}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}} + \frac{\alpha_3 f_3'(t)(x_2 - x_2^*)(x_4 - x_4^*)}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2}}$$
$$+\alpha_1 f_1'(t)(x_1 - x_1^*) \quad (4.53b)$$

$$\frac{dx_3}{dt} = \frac{\alpha_3 f_3'(t)(x_3 - x_3^*)(x_4 - x_4^*)}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2}}$$
$$-\alpha_2 f_2'(t)(\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2}) \quad (4.53c)$$

$$\frac{dx_4}{dt} = a_1 \alpha_3 f_3'(t) - \alpha_3 f_3'(t)(\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2}) \quad (4.53d)$$

These equations form the basis of this four variable model and their solution curves can be shown to satisfy the equation

$$\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2} - a_1 = \sqrt{a_2^2 - (x_4 - x_4^*)^2} \quad (4.54)$$

It is possible to find different forms of the four-dimensional torus and these are discussed in Chapter 6.

As in the previous analysis, both on the torus and the ellipsoid, there are many possible models from this one base model. One such model is examined here. The behaviour of the solution curves on the three–dimensional model in the previous section will now once again provide a key to the solution of this model.

### 4.2.1 The Basic Four Variable Model

As in the previous sections at this stage in the model formulation choices for $f_2'(t)$ and $f_3'(t)$ are made which instantly transform Equations 4.53 into a set resembling a workable model. The obvious choice is therefore to let

$$f_2'(t) = f_4(t)\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} \tag{4.55}$$

and

$$f_3'(t) = f_5(t)\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2} \tag{4.56}$$

where $f_4(t)$ and $f_5(t)$ are functions of time $t$.

Therefore the basic model becomes

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = \alpha_2 f_4(t)(x_1 - x_1^*)(x_3 - x_3^*) + \alpha_3 f_5(t)(x_1 - x_1^*)(x_4 - x_4^*) - \alpha_1 f_1'(t)(x_2 - x_2^*) \tag{4.57a}$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = \alpha_2 f_4(t)(x_2 - x_2^*)(x_3 - x_3^*) + \alpha_3 f_5(t)(x_2 - x_2^*)(x_4 - x_4^*) + \alpha_1 f_1'(t)(x_1 - x_1^*) \tag{4.57b}$$

$$\frac{\mathrm{d}x_3}{\mathrm{d}t} = \alpha_3 f_5(t)(x_3 - x_3^*)(x_4 - x_4^*) - \alpha_2 f_4(t)((x_1 - x_1^*)^2 + (x_2 - x_2^*)^2) \tag{4.57c}$$

$$\frac{\mathrm{d}x_4}{\mathrm{d}t} = a_1\alpha_3 f_5(t)(\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2})$$

$$-\alpha_3 f_5(t)((x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2) \tag{4.57d}$$

The simplest model for this four variable case is achieved by letting

$$f_1'(t) = 1 \tag{4.58}$$

$$f_4(t) = 1 \tag{4.59}$$

$$f_5(t) = 1 \tag{4.60}$$

This leads to the model

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = \alpha_2(x_1 - x_1^*)(x_3 - x_3^*) + \alpha_3(x_1 - x_1^*)(x_4 - x_4^*) - \alpha_1(x_2 - x_2^*) \tag{4.61a}$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = \alpha_2(x_2 - x_2^*)(x_3 - x_3^*) + \alpha_3(x_2 - x_2^*)(x_4 - x_4^*) + \alpha_1(x_1 - x_1^*) \tag{4.61b}$$

$$\frac{\mathrm{d}x_3}{\mathrm{d}t} = \alpha_3(x_3 - x_3^*)(x_4 - x_4^*) - \alpha_2((x_1 - x_1^*)^2 + (x_2 - x_2^*)^2) \tag{4.61c}$$

$$\frac{\mathrm{d}x_4}{\mathrm{d}t} = a_1\alpha_3(\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2})$$

$$-\alpha_3((x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2) \tag{4.61d}$$

The above set of equations could now be interpreted in terms of an ecosystem consisting of four species $x_1$, $x_2$, $x_3$ and $x_4$.

- $x_1$ grows from the presence of $x_3$ and $x_4$ and dies from the presence of $x_2$.
- $x_2$ grows from the presence of $x_1$, $x_3$ and $x_4$.
- $x_3$ grows from the presence of $x_4$ and dies from the presence of $x_1$ and $x_2$.
- $x_4$ dies from the presence of $x_1$, $x_2$ and $x_3$.

This system can therefore be described as consisting of a dominant omnivore, $x_2$, an omnivore, $x_1$, a herbivore, $x_3$ and a plant source, $x_4$. So, comparing it with the ecosystem modelled by the three-dimensional case, adding another dimension has had the effect of adding another member, an omnivore, to the food chain, in exactly the same manner as with the ellipsoid.

The three parameters $\alpha_1$, $\alpha_2$ and $\alpha_3$ are proportional to the rate of interaction between the four species.

- $\alpha_1$ is proportional to the rate of interaction between the two omnivores i.e. the death rate of the omnivore due to the predation by the more dominant omnivore and thus the growth rate of the dominant omnivore due to its predation of the less dominant one.
- $\alpha_2$ is proportional to the rate of interaction between the herbivore and the two omnivores i.e. the death rate of the herbivore due to predation by the omnivores and consequentially, the growth rate of the omnivores due to their predation of the herbivore.
- $\alpha_3$ is proportional to the rate of interaction between the plant source and the other three members of the ecosystem i.e. the 'death rate' of the plant source due to 'grazing' by the omnivores and the herbivore.

As in the three variable model it can be seen that there are two competing mechanisms for the plant source, one depleting it and the other replenishing it. This could be interpreted as regeneration of the plant source due to the presence of the other two species i.e. pollination, seed dispersal or fertilisation increasing the growth rate.

To enable analysis of how the time series for each variable behaves, it is useful at this stage to examine the fixed points of the system. From Equations 4.61a and b above, it can be seen that for when $x_1 = x_1^*$ and $x_2 = x_2^*$, $\frac{dx_1}{dt}$ and $\frac{dx_2}{dt} = 0$. From Equation 4.61d it follows that $\frac{dx_4}{dt} = 0$ when $x_3 = x_3^* \pm a_1$. Therefore, to satisfy $\frac{dx_3}{dt} = 0$, $x_4 = x_4^*$. Thus the system is stationary for the point $(x_1^*, x_2^*, x_3^* \pm a_1, x_4^*)$.

Since these fixed points differ from those found for the three-dimensional torus, it can be presumed that the solution curves will not behave in a similar manner to those of the three–dimensional torus. The nature of the point is again impossible to ascertain by the Jacobian Method due to the division by zero. The behaviour of the path might therefore be determined by examining $\theta_1$, $\theta_2$, and $\theta_3$.

The choices for $f_3'$, $f_2'$ and $f_1'$ lead to the following expressions for $\theta_3$, $\theta_2$ and $\theta_1$. Details can be found in Appendix B.

$$\theta_3 = 2\tan^{-1}\Big[\frac{\sqrt{a_1^2-a_2^2}}{a_1}\tan[\frac{\alpha_2\sqrt{a_1^2-a_2^2}}{2}(t+k_3)]-a_2\Big] \tag{4.62}$$

$$\theta_2 = 2\tan^{-1}\Big[\exp[\frac{\alpha_2}{\alpha_3}\theta_3+k_2]\Big] \tag{4.63}$$

$$\theta_1 = \alpha_1(t+k_1)+\phi_1 \tag{4.64}$$

It can be noted that $\theta_3$ in this model is the same as $\theta_2$ in the three–dimensional model (page 94). As $t$ is increasing at a constant rate then $\theta_3$ will never be constant. The original parametric equations for this four–dimensional torus were

$$x_1 - x_1^* = (a_1 + a_2\sin\theta_3)\sin\theta_2\cos\theta_1 \tag{4.65a}$$

$$x_2 - x_2^* = (a_1 + a_2\sin\theta_3)\sin\theta_2\sin\theta_1 \tag{4.65b}$$

$$x_3 - x_3^* = (a_1 + a_2\sin\theta_3)\cos\theta_2 \tag{4.65c}$$

$$x_4 - x_4^* = a_2\cos\theta_3 \tag{4.65d}$$

and it can therefore be surmised that $x_4$ will be constantly fluctuating around $x_4^*$.

$\theta_1$ for this model is also never constant and hence neither is $\sin\theta_1$ or $\cos\theta_1$. It is therefore $\theta_2$ which will determine how the system behaves. This proves difficult to do due to the complexity of it and the analysis of its behaviour and the consequences that this has on the solution curves must be the subject of future research.

Time series plots for various values of $\alpha_1$, $\alpha_2$ and $\alpha_3$ are shown below in Figures 4.20 to 4.22. Figure 4.20 shows the effect of varying $\alpha_1$, Figure 4.21 shows the effect of varying

$\alpha_2$ and Figure 4.22 shows the effect of varying $\alpha_3$. In all cases $a_1 = 10$, $a_2 = 5$, $x_1^* = 20$, $x_2^* = 20$, $x_3^* = 20$, $x_4^* = 20$.

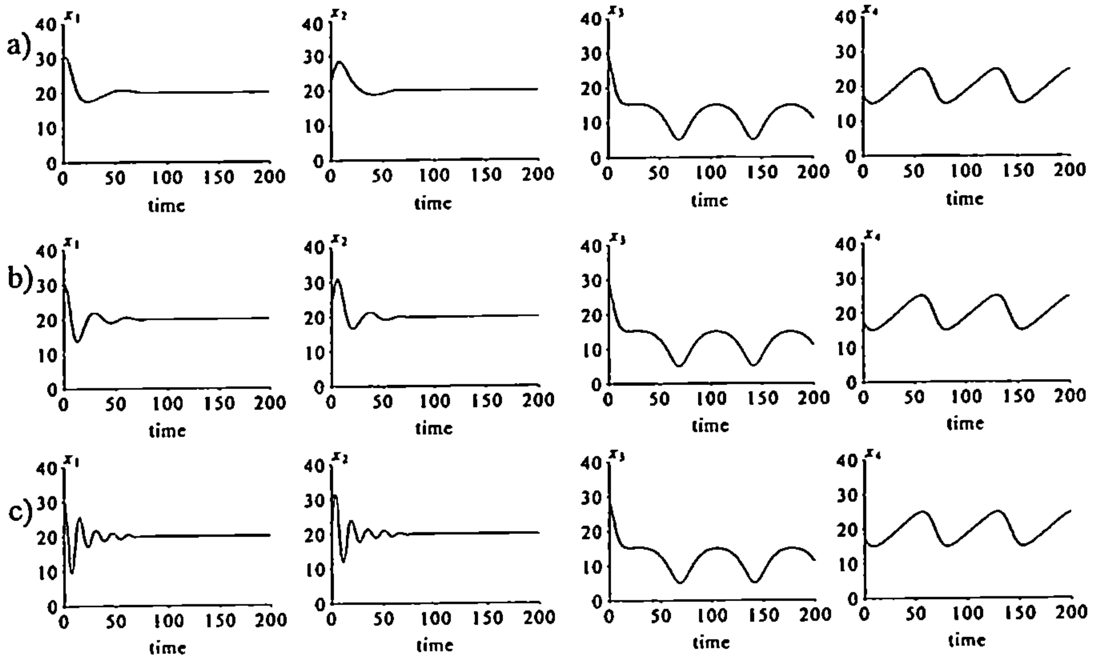


Figure 4.20: Solution curves of Equations 4.61 with $\alpha_2 = 0.01$, $\alpha_3 = 0.01$ and varying $\alpha_1$: a) $\alpha_1 = 0.1$, b) $\alpha_1 = 0.2$ and c) $\alpha_1 = 0.4$.

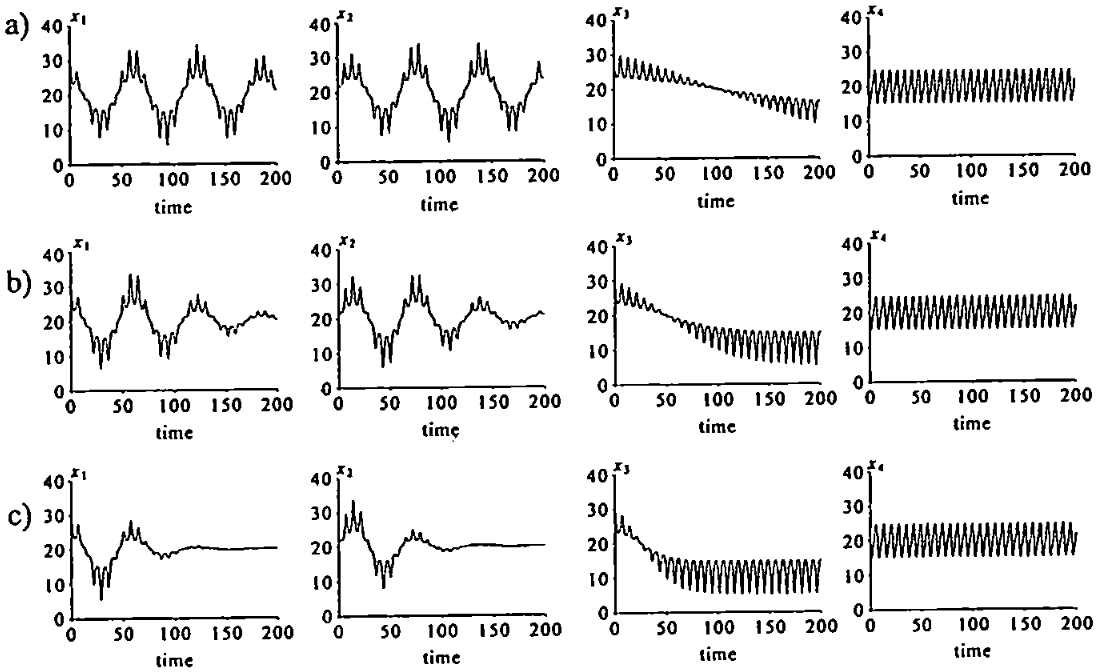


Figure 4.21: Solution curves of Equations 4.61 with $\alpha_1 = 0.1$, $\alpha_3 = 0.1$ and varying $\alpha_2$: a) $\alpha_2 = 0.001$, b) $\alpha_2 = 0.002$ and c) $\alpha_2 = 0.004$.

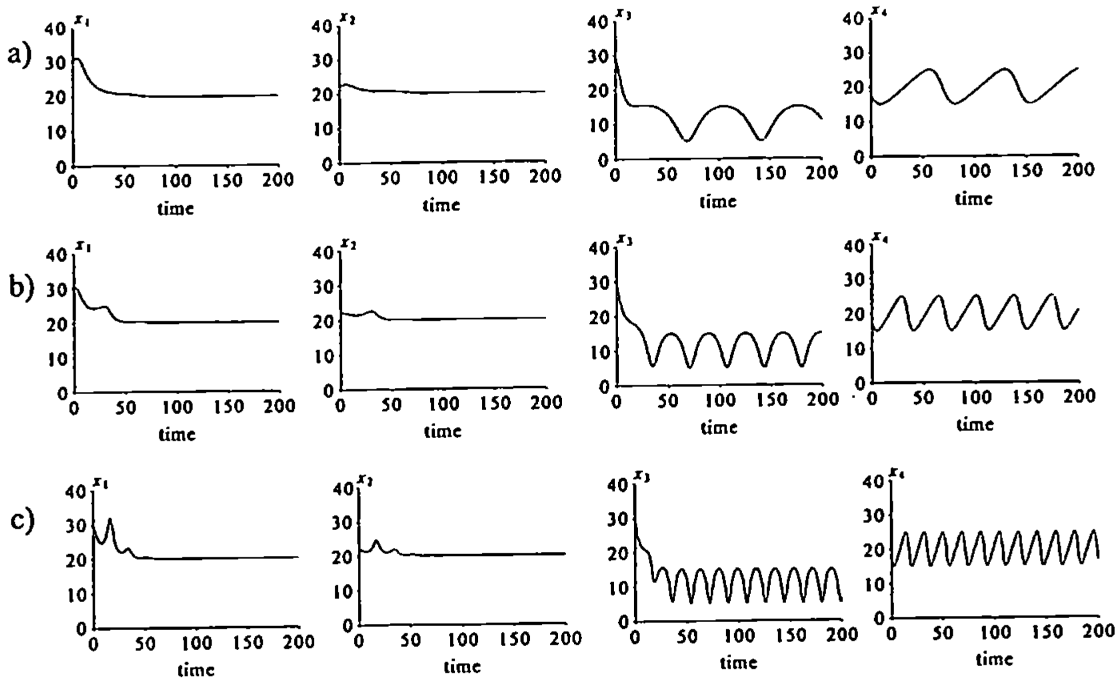


Figure 4.22: Solution curves of Equations 4.61 with $\alpha_1 = 0.001$, $\alpha_2 = 0.001$ and varying $\alpha_3$: a) $\alpha_3 = 0.001$, b) $\alpha_3 = 0.002$ and c) $\alpha_3 = 0.004$.

From the time series produced by solving Equations 4.61, it appears that $x_1$ and $x_2$ settle down to $x_1^*$ and $x_2^*$ respectively, $x_3$ fluctuates around $x_3^* - a_1$, and $x_4$ fluctuates around $x_4^*$ as predicted above. It appears from this that at some stage $\theta_2 = 2\pi n$, $n = \ldots -2, -1, 0, 1, 2 \ldots$. This would therefore cause $\sin\theta_2$ to equal 0 and thus $x_1 = x_1^*$ and $x_2 = x_2^*$, while allowing $x_3$ to continue fluctuating. However further work needs to be done on this.

It can be seen from these time series plots the effect of changing the three parameters, $\alpha_1$, $\alpha_2$ and $\alpha_3$. Increasing $\alpha_1$, which is the rate of interaction between $x_1$ and $x_2$, increases the number of fluctuations in the two population sizes. $\alpha_2$, which is the rate of interaction between $x_3$ and $x_1$ and $x_2$, has the similar effect as $\alpha_2$ had in the three dimensional torus. Increasing $\alpha_2$ increases the number of fluctuations of $x_3$ and therefore the number of small fluctuations in $x_1$ and $x_2$. It is similar to increasing the number of coils around the torus in the three-dimensional torus (page 96). Increasing $\alpha_3$, which is the rate of interaction between $x_4$ and $x_1$, $x_2$ and $x_3$, increases the number of fluctuations in $x_4$. This has a knock-on effect on the number of fluctuations in the other variables.

## 4.3 Summary

This chapter has looked at the torus as a surface on which to base a set of differential equations which model interacting populations. The three–dimensional torus provided interesting sets of models whose solutions could easily be interpreted because the surface was easy to visualise. The move from three–dimensions to four proved less successful than with the ellipsoid. The torus as a surface is far more complex than the ellipsoid due to the 'hole' in its middle. When this is translated into four–dimensions, it is less clear as to how it behaves. However the analysis done on the three dimensional torus proved useful in predicting how the four variable model might behave. It will be more detailed analysis of the higher dimensional torus that will lead to future work in this subject.

# Chapter 5

# Evaluation of the Geometric Approach to Modelling Interacting Populations

## 5.1 Introduction

This chapter discusses the use of the type of model introduced in this thesis. It addresses some of the advantages of using a geometric approach over the traditional method of model formulation. No model, however detailed, is perfect and this geometric formulation is no exception. Therefore in this chapter there will be a discussion of the disadvantages of this approach.

## 5.2 Advantages of the Geometric Approach to Modelling

### 5.2.1 Visualisation

In essence, any two variable model produces a series of points to form a curve on a plane. Similarly any three variable model can produce a series of points to form a curve on a surface. This geometric approach has simply constrained the surface to one which can be expressed by a set of parametric equations and, more importantly, to one which can be visualised. It is this ability to visualize the motion of the curve on the surface that enables this style of approach to be a powerful tool. It allows the interaction between each variable to be understood in a far more detailed and constructive manner than simply a set of equations can provide.

For example, consider again the first model studied, model 1 for the 3 dimensional ellipsoid on page 55. The interaction between $x_1$, the herbivore and $x_3$, the plant source and similarly that between $x_2$, the omnivore and the plant source, can be interpreted and understood easily simply because the interaction of all *three* variables can be visualised together. It can be seen that as the plant source decreases, i.e. as the path moves down the ellipsoid, the range of the fluctuations in the omnivore and herbivore at first increase to a maximum (half way down) when the available plant source can support the maximum herbivore population which therefore can support the maximum omnivore population. However as the plant source is depleted further, the fluctuations become smaller which can easily be visualised by the narrowing of the ellipsoid. The stationary point at the bottom of the ellipsoid represents no fluctuations in any of the populations, again easy to interpret by picturing the path on the surface as having nowhere to go.

With well known surfaces such as the two considered here, the ability to see an overall picture allows a far better understanding of the whole system. Even with relatively simple three variable models constructed along the traditional lines, the interaction between each component is not easy to understand. A set of equations cannot tell the whole picture, the interaction between two variables is simply a term in an equation. By having a visual representation of this interaction, it allows the intelligent layperson to interpret the outcomes. The ability to obtain a picture of the *whole* system is one of the most important and innovative outcomes of this approach.

The ability to visualize the basic model assists greatly with the analysis of those created from this elementary idea especially when the concept is extended to higher dimensions.

The patterns which emerge from the three–dimensional models and which are repeated in higher dimensions can be understood and interpreted in far more detail. This would not be so easy if the basic building blocks were simply a set of equations without an overall picture.

### 5.2.2 Control

One of the concerns facing many modellers is the effect of parameter changes. With the large scale models presently being formulated, it is very easy to lose control over the effects of such changes. Often the parameters are 'tweaked' constantly in order to fit a certain variable to data without much notice of the effect such changes have on the other components of the model. It can lead to a vicious circle, changing one parameter can call for the need to change another, then another and often the first one again. This geometric approach to model formulation allows a tighter control over the effects of any changes. All the parameters in the models are those which characterise the surfaces or effect the motion of the path on the surface. By changing any one of the parameters, the effect on all variables in the model is instantly known. For example by changing the height of the ellipsoid (controlled by $a_3$) its effects on all the variables are known because the basic path must remain the same, the omnivore and herbivore will still fluctuate but with larger period since the available plant source is larger to start with.

For the torus, if a periodic cycle (as formulated on page 90) is required it limits the number of free parameters to only those which describe the shape of the torus. By having all parameters linked to each other in this way allows further control over any changes that may be made. By altering $a_2$, the parameter which controls the 'fatness' of the torus, the size of the fluctuations caused by the interaction between the omnivore and the herbivore will increase. The modeller can both visualize and interpret the result on the variables without need for detailed examination of the results. The effect that altering one parameter will have on *all* variables is immediately obvious.

### 5.2.3 Adaptability

Many critics may presume that the models are too simplistic. However this apparently simple design hides a wealth of possibilities. For the three–dimensional ellipsoid the basic model was

$$\frac{dx_1}{dt} = \frac{\alpha_2 f_3(t)}{a_3}(x_1 - x_1^*)(x_3 - x_3^*) - \frac{a_1\alpha_1 f_1'(t)}{a_2}(x_2 - x_2^*) \quad (5.1a)$$

$$\frac{dx_2}{dt} = \frac{\alpha_2 f_3(t)}{a_3}(x_2 - x_2^*)(x_3 - x_3^*) + \frac{a_2\alpha_1 f_1'(t)}{a_1}(x_1 - x_1^*) \quad (5.1b)$$

$$\frac{dx_3}{dt} = -a_3\alpha_2 f_3(t)(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}) \quad (5.1c)$$

and for the three–dimensional torus...

$$\frac{dx_1}{dt} = \alpha_1 f_3(t)(x_1 - x_1^*)(x_3 - x_3^*) - \alpha_2 f_2'(t)(x_2 - x_2^*) \quad (5.2a)$$

$$\frac{dx_2}{dt} = \alpha_1 f_3(t)(x_2 - x_2^*)(x_3 - x_3^*) + \alpha_2 f_2'(t)(x_1 - x_1^*) \quad (5.2b)$$

$$\frac{dx_3}{dt} = a_1\alpha_1 f_3(t)\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} - \alpha_1 f_3(t)((x_1 - x_1^*)^2 + (x_2 - x_2^*)^2). \quad (5.2c)$$

It is the inclusion of the functions, $f_1'(t)$ and $f_3(t)$ for the ellipsoid, $f_2'(t)$ and $f_3(t)$ for the torus, that allows this approach to model formulation to be used for a wide range of situations. The functions can be *any* function of $t$, (and thus a function of any of the variables in the system), and the solution curve will still remain on the chosen surface. Only a small number of all possible functions were studied in depth here but the potential number available would allow the basic models to be adaptable to many situations.

### 5.2.4 Extendibility

A further illustration of the advantages of this technique is the relative ease in extending to higher dimensions. This is particularly true for the ellipsoid since in higher dimensions it remains simply connected. In setting up the basic three–dimensional model for the ellipsoid and then adding a further variable the patterns in the equations are obvious. It is easy to then simply write down the set of differential equations for a 5 variable system or higher. The general model for a 5 variable system is

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = \frac{\alpha_2 f_5(t)}{a_3}(x_1 - x_1^*)(x_3 - x_3^*) + \frac{\alpha_3 f_6(t)}{a_4}(x_1 - x_1^*)(x_4 - x_4^*)$$

$$+\frac{\alpha_4 f_7(t)}{a_5}(x_1 - x_1^*)(x_5 - x_5^*) - \frac{a_1\alpha_1 f_1'(t)}{a_2}(x_2 - x_2^*) \tag{5.3a}$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = \frac{\alpha_2 f_5(t)}{a_3}(x_2 - x_2^*)(x_3 - x_3^*) + \frac{\alpha_3 f_6(t)}{a_4}(x_2 - x_2^*)(x_4 - x_4^*)$$

$$+\frac{\alpha_4 f_7(t)}{a_5}(x_2 - x_2^*)(x_5 - x_5^*) + \frac{a_1\alpha_1 f_1'(t)}{a_2}(x_1 - x_1^*) \tag{5.3b}$$

$$\frac{\mathrm{d}x_3}{\mathrm{d}t} = \frac{\alpha_3 f_6(t)}{a_4}(x_3 - x_3^*)(x_4 - x_4^*) + \frac{\alpha_4 f_7(t)}{a_5}(x_3 - x_3^*)(x_5 - x_5^*)$$

$$-a_3\alpha_2 f_5(t)\left(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}\right) \tag{5.3c}$$

$$\frac{\mathrm{d}x_4}{\mathrm{d}t} = \frac{\alpha_4 f_7(t)}{a_5}(x_4 - x_4^*)(x_5 - x_5^*)$$

$$-a_4\alpha_3 f_6(t)\left(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2}\right) \tag{5.3d}$$

$$\frac{\mathrm{d}x_5}{\mathrm{d}t} = -a_5\alpha_4 f_7(t)\left(\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2} + \frac{(x_4 - x_4^*)^2}{a_4^2}\right) \tag{5.3e}$$

where $f_5(t)$, $f_6(t)$ and $f_7(t)$ are the functions of $t$. The relative ease at which the step from three–dimensions to four in the case of the ellipsoid was made, helped when considering the torus. With the ellipsoid the general equation,

$$\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2} = 1 \tag{5.4}$$

extends readily to higher dimensions. However with the torus,

$$\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} - a_1 = \sqrt{a_2^2 - (x_3 - x_3^*)^2)} \tag{5.5}$$

there are alternative ways to extend into four–dimensions. It was the work done with the parametric equations for the ellipsoid that allowed a connection to be made. By examining the pattern between the two sets, Equations 3.2 and 3.39. a similar extension could then be applied to the parametric equations for the torus. This pattern is shown in Figure 5.1.

$$\begin{array}{l} x_1 - x_1^* = a_1 \sin\theta_2 \cos\theta_1 \\ x_2 - x_2^* = a_2 \sin\theta_2 \sin\theta_1 \\ x_3 - x_3^* = a_3 \cos\theta_2 \end{array} \longrightarrow \begin{array}{l} x_1 - x_1^* = a_1 \sin\theta_3 \sin\theta_2 \cos\theta_1 \\ x_2 - x_2^* = a_2 \sin\theta_3 \sin\theta_2 \sin\theta_1 \\ x_3 - x_3^* = a_3 \sin\theta_3 \cos\theta_2 \\ x_4 - x_4^* = a_4 \cos\theta_3 \end{array}$$

(a)

$$\begin{array}{l} x_1 - x_1^* = (a_1 + a_2 \sin\theta_2) \cos\theta_1 \\ x_2 - x_2^* = (a_1 + a_2 \sin\theta_2) \sin\theta_1 \\ x_3 - x_3^* = a_2 \cos\theta_2 \end{array} \longrightarrow \begin{array}{l} x_1 - x_1^* = (a_1 + a_2 \sin\theta_3) \sin\theta_2 \cos\theta_1 \\ x_2 - x_2^* = (a_1 + a_2 \sin\theta_3) \sin\theta_2 \sin\theta_1 \\ x_3 - x_3^* = (a_1 + a_2 \sin\theta_3) \cos\theta_2 \\ x_4 - x_4^* = a_2 \cos\theta_3 \end{array}$$

(b)

Figure 5.1: Similarities and extension of the parametric equations for (a) the ellipsoid and (b) the torus

It was then by following the same techniques in finding expressions for $\sin\theta_1$, $\cos\theta_2$ that the general expression for one version of the four dimensional torus could be obtained. The appearance of $\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2}$ led to the assumption that this expression must appear in the general equation i.e.

$$\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2} - a_1 = \sqrt{a_2^2 - (x_4 - x_4^*)^2} \tag{5.6}$$

Other expressions for four–dimensional torii are discussed in Chapter 6.

Even though some of the analysis of the higher dimensional models may not be completed in sufficient depth it is still possible to understand how the system will act. For example it was possible to achieve a detailed analysis of the angles $\theta_1$ and $\theta_2$ in the basic three dimensional ellipsoid. This gave an extremely good insight to how the solution curve would behave in the four–dimensional case. This allows the ideas and concepts which can be understood and analysed fully to be extended to the higher dimensions, even when the mathematical analysis is either not possible to do exactly or is too complex to be understood.

### 5.2.5 Application to Interacting Populations

As discussed for each model the set of differential equations can be interpreted in terms of interacting populations. All the three variable models can represent an ecosystem consisting of a herbivore, an omnivore and a plant source. The choices that were made for the arbitrary functions $f_i(t)$ produced variations that allowed different situations to be proposed. There are types of ecosystems that this modelling technique could be applied to, for example, zooplankton, phytoplankton and a nutrient source, and such a system is modelled by the basic three dimensional torus model, Sharp & Dyke 1995.

The extension into four variables introduced a dominant omnivore into the ecosystem. Equations 5.3 for a five variable system can be interpreted in terms of an ecosystem consisting of five species $x_1$, $x_2$, $x_3$, $x_4$ and $x_5$.

- $x_1$ grows from the presence of $x_3$, $x_4$ and $x_5$ and dies from the presence of $x_2$.
- $x_2$ grows from the presence of $x_1$, $x_3$, $x_4$ and $x_5$.
- $x_3$ grows from the presence of $x_4$ and $x_5$ and dies from the presence of $x_1$ and $x_2$.
- $x_4$ grows from the presence of $x_5$ and dies from the presence of $x_1$, $x_2$ and $x_3$.
- $x_5$ dies from the presence of $x_1$, $x_2$, $x_3$ and $x_4$.

Therefore adding a further variable has the effect of adding another omnivore to the system, in effect setting up a food chain. This extension of the chain with each additional variable is illustrated in Figure 5.2 overleaf.

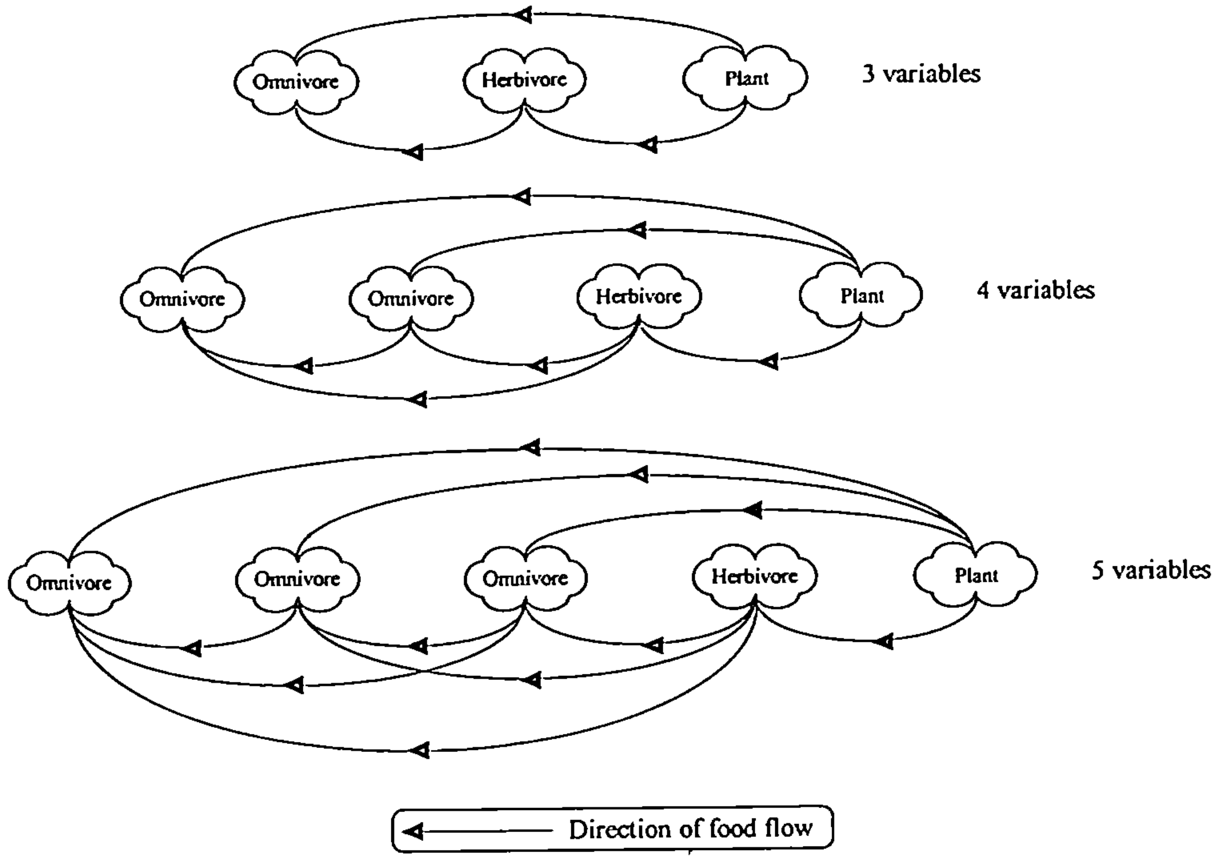


Figure 5.2: The effect of adding further variables to the ellipsoid model

### 5.2.6 Learning Tools

Many scientists do not have a mathematical background yet are expected to use quite complex mathematics to build mathematical models. The approach to modelling presented in this thesis can be used as an effective tool in assisting those individuals. Indeed the same could be applied to mathematics students tackling the subject of modelling with differential equations for the first time.

Knowing how a system behaves without the need for detailed mathematical knowledge allows the important issues to be examined. As previously mentioned, the effects of parameter change plays a large part in many models. Simple models such as the three-dimensional ellipsoid or torus can be experimented upon and the effects of the parameter changes noted. Once this has been mastered then a more complex or realistic model can be built from these basic ones. It was indeed this method which allowed the analysis of the different models to be examined in the previous chapters. It was possible to obtain a very detailed analysis of the behaviour and then build on this when formulating and analysing the later models.

Therefore this type of model formulation can provide a very useful tool to add to those already used by modellers. The modellers will benefit from the knowledge that it is possible to view the system as a whole and not individual solution curves. Even if the final model has digressed from a geometric one the skills learnt in formulating such models can still be applied. By observing the interaction of two or three variables together may lead to a better understanding of the system as a whole.

## 5.3 Disadvantages of the Geometric Approach to Modelling

### 5.3.1 Unusual Terms

One of the criticisms received about these models is the unusual terms in the differential equations. Admittedly it is rare to find terms such as $\sqrt{x_1 + x_2}$ in a set of differential equations to represent an interaction with $x_1$ and $x_2$. However, these terms arise from the formulation of the model, it is one of the restrictions of the geometric approach. Conventional modellers may worry about such terms simply because they have never been used to represent the interactions before. The convention is to use linear or quasi-linear interaction terms for numerical ease. It could be argued that real life is not as simple as they may wish, the more complex terms which geometric types of models produce may in fact be better at representing real life; real life is certainly not linear.

### 5.3.2 Analysing Four–dimensional Shapes

Although the transfer from the three to the four–dimensional ellipsoid was relatively straightforward, the torus proved more difficult. This was due to the more complex nature of the torus. The analysis of how the solution curves behaved on the four–dimensional torus was hindered by the inability to really understand what the surface looked like as well as the complicated mathematics that resulted from the model. However it should be noted that comparing the time series plots for this model to those of the three dimensional one did assist in explaining some of the details.

## 5.4 Summary

It is been the aim of this thesis to present the idea of the geometric approach to the formulation of mathematical models. However it is also important to address some of the issues arising from such an approach and this chapter has attempted to do that. Such models have a number of benefits; the visualisation of the whole system, the control over the parameters, the wide range of different models that can be produced from the basic one, the relative ease of extension into higher dimensions and maybe most importantly, the opportunity to use such models as learning tools. The few drawbacks of such models have also been noted, their restricted use and the unusual appearance of the equations. The next chapter outlines some of the work that can still be done in this area.

# Chapter 6

# Future Work and Conclusions

## 6.1 Introduction

This final chapter outlines some of the future work that can be done on this topic. This thesis has only covered a small part of what has turned out to be a very large topic. There are many opportunities for this work to be extended. One such extension is the study of different expressions for the higher dimensional torus. Another is the huge range of models that can be explored by allowing further choices for the arbitrary functions in each general model. These extensions are discussed briefly in this chapter.

## 6.2 Future Work

### 6.2.1 Other Four–dimensional Tori

As mentioned in Chapter 5, there are alternative ways to extend the three–dimensional torus into four–dimensions. It was by examining the pattern of the parametric equations that led to the one which has been studied in this thesis. However other general equations do exist for such four–dimensional shapes.

One of these is

$$\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} - a_1 = \sqrt{a_2^2 - (x_3 - x_3^*)^2 - (x_4 - x_4^*)^2)}. \tag{6.1}$$

This version can be parameterised by

$$x_1 - x_1^* = (a_1 + a_2 \sin\theta_3)\cos\theta_1 \tag{6.2a}$$

$$x_2 - x_2^* = (a_1 + a_2 \sin\theta_3)\sin\theta_1 \tag{6.2b}$$

$$x_3 - x_3^* = a_2 \cos\theta_3 \cos\theta_2 \tag{6.2c}$$

$$x_4 - x_4^* = a_2 \cos\theta_3 \sin\theta_2 \tag{6.2d}$$

Some preliminary work has already been done and the general model is found to be

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = \frac{\alpha_3 f_3'(t)(x_1 - x_1^*)\sqrt{(x_3 - x_3^*)^2 + (x_4 - x_4^2)}}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^2)}} - \alpha_1 f_1'(t)(x_2 - x_2^*) \tag{6.3a}$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = \frac{\alpha_3 f_3'(t)(x_2 - x_2^*)\sqrt{(x_3 - x_3^*)^2 + (x_4 - x_4^2)}}{\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^2)}} + \alpha_1 f_1'(t)(x_1 - x_1^*) \tag{6.3b}$$

$$\begin{aligned}\frac{\mathrm{d}x_3}{\mathrm{d}t} &= \frac{a_1 \alpha_3 f_3'(t)(x_3 - x_3^*)}{\sqrt{(x_3 - x_3^*)^2 + (x_4 - x_4^2)}} - \alpha_2 f_2'(t)(x_4 - x_4^*) \\ &\quad - \frac{\alpha_3 f_3'(t)(x_3 - x_3^*)\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^2)}}{\sqrt{(x_3 - x_3^*)^2 + (x_3 - x_3^2)}}\end{aligned} \tag{6.3c}$$

$$\begin{aligned}\frac{\mathrm{d}x_4}{\mathrm{d}t} &= \frac{a_1 \alpha_3 f_3'(t)(x_4 - x_4^*)}{\sqrt{(x_3 - x_3^*)^2 + (x_4 - x_4^2)}} + \alpha_2 f_2'(t)(x_3 - x_3^*) \\ &\quad - \frac{\alpha_3 f_3'(t)(x_4 - x_4^*)\sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^2)}}{\sqrt{(x_3 - x_3^*)^2 + (x_3 - x_3^2)}}\end{aligned} \tag{6.3d}$$

It can be seen that although some similarities to the original four–dimensional torus exist, the set of differential equations that make up this model have some noticeable differences. This may lead to a different type of behaviour of the solution paths. This model can be examined in the same detail as that presented in Chapter 4.

### 6.2.2 Many More Models

The work presented in this thesis has been limited to a small number of models for each surface studied. There are many further models that can be obtained by simply allowing different choices for the arbitrary functions $f_i(t)$ that appear in all the models. The functions in this case have been chosen to illustrate the idea of the geometric approach. Further work can be done by examining some of the models produced when other functions are chosen.

### 6.2.3 Applying the Models

Although this thesis has concentrated on the mathematics of modelling through a geometric approach, one of the main aims for future work is to apply the models generated to real life situations. The types of models generated can be applied to any herbivore, omnivore, plant situation. For some appropriate data the model could be tailored to fit the situation by choosing different functions as mentioned above. This would be the validation stage of the modelling cycle which is very important if the work done in this thesis is to have any real applications.

## 6.3 Conclusion

At the beginning of the period of study for this thesis, the ideas of modelling physical situations by differential equations had been based on hands on experience. Working with a mathematical modeller of marine ecosystems for a few months encouraged an interest in the formulation of such models. Much time was spent 'tweaking' parameter values in order for the model to fit the data. Changing one parameter caused the need to change another, then another and often the first one again. This frustrating aspect of model formulation led to this study of a geometric approach to mathematical modelling. If the feeling of 'loss of control' over a model could be reduced in any way then that had to be a bonus. This thesis presents this approach in order to illustrate how to build geometrically based models and some of the possible outcomes of the solutions.

The idea for the geometric approach was conceived when investigating the well known predator prey model in order to achieve a good understanding of the concepts of the underlying mathematics. The solution to the model can be shown to lay on an ellipse under certain conditions. This led to the realisation that all two variable models produced solution curves that followed a path in two dimensions, sometimes the general equation of this path could be found, in others it could not. All three variable models therefore followed a path on a three–dimensional surface. If the equation of that surface was known then the path taken by the solution curves could be fully understood. Therefore the geometric approach was born: start with a surface whose equation was known and develop a differential equation model from it.

It is well known that the 'visualisation' of mathematics can greatly enhance the understanding of the concepts behind it. The same can be applied to the modelling process; if the outcomes can be visualised in a meaningful way then that surely must improve the understanding of the mathematics. With well known surfaces such as the two considered here, the ability to see an overall picture allows a far better understanding of the whole system. A set of equations cannot tell the whole picture, the interaction between two variables is simply a term in an equation. The ability to obtain a picture of the *whole* system is one of the most important and innovative outcomes of this approach.

The ability to visualize the basic model assists greatly with the analysis of those created from this elementary idea especially when the concept is extended to higher dimensions. The patterns which emerge from the three–dimensional models and which are repeated in higher dimensions can be understood and interpreted in far more detail. This would not be so easy if the basic building blocks were simply a set of equations without an overall picture.

This study has provided a thorough understanding of the mathematical concepts behind differential equation modelling and has shown an innovative approach to the formulation of such models. It has been a study full of pleasant surprises; the sets of equations could actually be interpreted in terms of a ecosystem, the ellipsoid readily extended into higher dimensions, the mathematics was easy to interpret due to the ability to visualise the 'whole'. It also had its disappointments; the difficulty in analysing fully the higher dimensional torus being the main one. However such difficulties led to a eagerness to solve the problem in the future. This study has been explicitly on the mathematics behind the geometrical approach and has covered the topic in depth. The next step will be the application of such models to real situations, only then will this topic be complete.

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# Appendix A

# Integration of Functions in Chapter 3

## A.1 The Ellipsoid

In Chapter 3, Section 3.2 the functions $f_1(t)$ and $f_2(t)$ were found by integrating the chosen expressions for $f_1'(t)$ and $f_2'(t)$. Here these integrations are shown with more detail. In each of the three models $f_3(t)$=1 and so

$$f_2'(t) = \sqrt{\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}} \tag{A.1}$$

$$= \sin(\alpha_2 f_2(t) + \phi_2) \tag{A.2}$$

from Equations 3.6 on page 52. Therefore

$$\int \frac{\mathrm{d}f_2(t)}{\sin(\alpha_2 f_2(t) + \phi_2)} = \int \mathrm{d}t. \tag{A.3}$$

Considering the left hand side of Equation A.3 let $p = \tan(\frac{\alpha_2 f_2(t)+\phi_2}{2})$ and so

$$\int \frac{\mathrm{d}f_2(t)}{\sin(\alpha_2 f_2(t) + \phi_2)} = \frac{1}{\alpha_2}\int \frac{\mathrm{d}p}{p} \tag{A.4}$$

$$= \frac{1}{\alpha_2} \ln p \tag{A.5}$$

$$= \frac{1}{\alpha_2} \ln(\tan(\frac{\alpha_2 f_2(t) + \phi_2}{2})) \tag{A.6}$$

Therefore Equation A.3 becomes

$$\frac{1}{\alpha_2} \ln(\tan(\frac{\alpha_2 f_2(t) + \phi_2}{2})) = t + k_2 \tag{A.7}$$

where $k_2$ is the constant of integration. Therefore in all three models

$$\alpha_2 f_2(t) + \phi_2 = 2 \tan^{-1}(\mathrm{e}^{\alpha_2(t+k_2)}) \tag{A.8}$$

**Model 2**

In this model the choice of $f_1(t)$ was such that

$$f_1'(t) = (x_1 - x_1^*)(x_2 - x_2^*) \tag{A.9}$$

$$= a_1 a_2 \sin^2(\alpha_2 f_2(t) + \phi_2) \cos(\alpha_1 f_1(t) + \phi_1) \sin(\alpha_1 f_1(t) + \phi_1) \tag{A.10}$$

and so

$$\int \frac{\mathrm{d}f_1}{\cos(\alpha_1 f_1(t) + \phi_1) \sin(\alpha_1 f_1(t) + \phi_1)} = \int a_1 a_2 \sin^2(\alpha_2 f_2(t) + \phi_2) \mathrm{d}t \tag{A.11}$$

Consider the left handside of Equation A.11 and let $p = \tan(\frac{\alpha_1 f_1(t) + \phi_1}{2})$. Therefore

$$\int \frac{\mathrm{d}f_1}{\cos(\alpha_1 f_1(t) + \phi_1) \sin(\alpha_1 f_1(t) + \phi_1)} = \frac{1}{\alpha_1} \int \frac{1 + p^2}{p(1 - p^2)} \mathrm{d}p \tag{A.12}$$

$$= \frac{1}{\alpha_1} \int (\frac{1}{p} + \frac{2p}{1 - p^2}) \mathrm{d}p \tag{A.13}$$

$$= \frac{1}{\alpha_1} (\ln(p) - \ln(1 - p^2)) \tag{A.14}$$

$$= \frac{1}{\alpha_1} \ln(\frac{p}{1-p^2}) \quad (A.15)$$

$$= \frac{1}{\alpha_1} \ln(\frac{\tan(\frac{\alpha_1 f_1(t)+\phi_1}{2})}{1-\tan^2(\frac{\alpha_1 f_1(t)+\phi_1}{2})}) \quad (A.16)$$

$$= \frac{1}{\alpha_1} \ln(\frac{1}{2}\tan(\alpha_1 f_1(t)+\phi_1)) \quad (A.17)$$

Now the right hand side of Equation A.11 can be rewritten using Equation A.8 as

$$\int a_1 a_2 \sin^2(\alpha_2 f_2(t)+\phi_2)\mathrm{d}t = \int a_1 a_2 \sin^2\Big(2\tan^{-1}(\mathrm{e}^{\alpha_2(t+k_2)})\Big)\mathrm{d}t \quad (A.18)$$

$$= 4a_1a_2 \int \frac{\mathrm{e}^{2\alpha_2(t+k_2)}}{(\mathrm{e}^{2\alpha_2(t+k_2)}+1)^2}\mathrm{d}t \quad (A.19)$$

$$= \frac{-2a_1a_2}{\alpha_2(\mathrm{e}^{2\alpha_2(t+k_2)}+1)} \quad (A.20)$$

Therefore

$$\frac{1}{\alpha_1} \ln(\frac{1}{2}\tan(\alpha_1 f_1(t)+\phi_1)) = \frac{-2a_1a_2}{\alpha_2(\mathrm{e}^{2\alpha_2(t+k_2)}+1)} \quad (A.21)$$

and so

$$\alpha_1 f_1(t)+\phi_1 = \tan^{-1}(2\mathrm{e}^{-2\alpha_1/\alpha_2(\mathrm{e}^{2\alpha_2(t+k_2)+1})}). \quad (A.22)$$

**Model 3**

In this model the choice of $f_1(t)$ was such that

$$f_1'(t) = (x_1 - x_1^*) + (x_2 - x_2^*) \quad (A.23)$$

$$= \sin(\alpha_2 f_2(t)+\phi_2)(a_1\cos(\alpha_1 f_1(t)+\phi_1) + a_2\sin(\alpha_1 f_1(t)+\phi_1)) \quad (A.24)$$

and so

$$\int \frac{\mathrm{d}f_1}{a_1\cos(\alpha_1 f_1(t)+\phi_1)+a_2\sin(\alpha_1 f_1(t)+\phi_1)} = \int \sin(\alpha_2 f_2(t)+\phi_2)\mathrm{d}t \quad (A.25)$$

Consider the left hand side of Equation A.25 and again let $p = \tan(\frac{\alpha_1 f_2(t)+\phi_1}{2})$. Therefore

$$\int \frac{df_1}{a_1\cos(\alpha_1 f_1(t)+\phi_1)+a_2\sin(\alpha_1 f_1(t)+\phi_1)} = \frac{2}{\alpha_1}\int \frac{dp}{a_1(1-p^2)+2a_2 p} \quad \text{(A.26)}$$

$$= \frac{-2}{\alpha_1}\int \frac{dp}{(\frac{p-a_2}{a_1})^2 - (\frac{\sqrt{a_1^2+a_2^2}}{a_1})^2} \quad \text{(A.27)}$$

$$= \frac{-a_1}{\alpha_1\sqrt{a_1^2+a_2^2}}\ln(\frac{a_1 p - a_2 - \sqrt{a_1^2+a_2^2}}{a_1 p - a_2 + \sqrt{a_1^2+a_2^2}}) \quad \text{(A.28)}$$

$$= \frac{-a_1}{\alpha_1\sqrt{a_1^2+a_2^2}}\ln(\frac{a_1\tan(\frac{\alpha_1 f_1(t)+\phi_1}{2}) - a_2 - \sqrt{a_1^2+a_2^2}}{a_1\tan(\frac{\alpha_1 f_1(t)+\phi_1}{2}) - a_2 + \sqrt{a_1^2+a_2^2}}) \quad \text{(A.29)}$$

The right hand side of Equation A.25 becomes

$$\int \sin(\alpha_2 f_2(t)+\phi_2)dt = \int \sin\Big(2\tan^{-1}(e^{\alpha_2(t+k_2)})\Big)dt \quad \text{(A.30)}$$

$$= 2\int \frac{e^{2\alpha_2(t+k_2)}}{e^{2\alpha_2(t+k_2)}+1}dt \quad \text{(A.31)}$$

$$= \frac{2}{\alpha_2}\tan^{-1}(e^{2\alpha_2(t+k_2)}). \quad \text{(A.32)}$$

Therefore Equation A.25 becomes

$$\frac{-a_1}{\alpha_1\sqrt{a_1^2+a_2^2}}\ln(\frac{a_1\tan(\frac{\alpha_1 f_1(t)+\phi_1}{2}) - a_2 - \sqrt{a_1^2+a_2^2}}{a_1\tan(\frac{\alpha_1 f_1(t)+\phi_1}{2}) - a_2 + \sqrt{a_1^2+a_2^2}}) = \frac{2}{\alpha_2}\tan^{-1}(e^{2\alpha_2(t+k_2)}). \quad \text{(A.33)}$$

## A.2 Four–dimensional Ellipsoid

In the four–dimensional model there are three functions, $f_1(t)$, $f_2(t)$ and $f_3(t)$. $f_2(t)$ and $f_3(t)$ are the same in all three models and the integration to obtain these functions is shown below.

$$f_3'(t) = \sqrt{\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2} + \frac{(x_3 - x_3^*)^2}{a_3^2}} \quad (A.34)$$

$$= \sin(\alpha_3 f_3(t) + \phi_3) \quad (A.35)$$

from Equations 3.42 on page 72. Therefore

$$\int \frac{\mathrm{d}f_3(t)}{\sin(\alpha_3 f_3(t) + \phi_3)} = \int \mathrm{d}t. \quad (A.36)$$

Using the same procedure as above for $f_2(t)$ in the ellipsoid (equations A.3 to A.8) an expression for $f_3(t)$ can be found to be

$$\alpha_3 f_3(t) + \phi_3 = 2\tan^{-1}(\mathrm{e}^{\alpha_3(t+k_3)}) \quad (A.37)$$

where $k_3$ is the constant of integration.

An expression for $f_2(t)$ can also be found as follows

$$f_2'(t) = \sqrt{\frac{(x_1 - x_1^*)^2}{a_1^2} + \frac{(x_2 - x_2^*)^2}{a_2^2}} \quad (A.38)$$

$$= \sin(\alpha_2 f_2(t) + \phi_2)\sin(\alpha_3 f_3(t) + \phi_3) \quad (A.39)$$

from Equations 3.42 on page 72. Therefore

$$\int \frac{\mathrm{d}f_2(t)}{\sin(\alpha_2 f_2(t) + \phi_2)} = \int \sin(\alpha_3 f_3(t) + \phi_3)\mathrm{d}t \quad (A.40)$$

$$\frac{1}{\alpha_2}\ln(\tan(\frac{\alpha_2 f_2(t) + \phi_2}{2})) = \int \sin(\alpha_3 f_3(t) + \phi_3)\mathrm{d}t. \quad (A.41)$$

Consider the right hand side of Equation A.41.

$$\int \sin(\alpha_3 f_3(t) + \phi_3)\mathrm{d}t = \int \sin(2\tan^{-1}(\mathrm{e}^{\alpha_3(t+k_3)})) \tag{A.42}$$

$$= \int \frac{2\mathrm{e}^{\alpha_3(t+k_3)}}{\mathrm{e}^{\alpha_3(t+k_3)} + 1}\mathrm{d}t. \tag{A.43}$$

Let $\mathrm{e}^{\alpha_3(t+k_3)} = u$ and therefore

$$\int \sin(\alpha_3 f_3(t) + \phi_3)\mathrm{d}t = \frac{2}{\alpha_3}\int \frac{1}{u^2+1}\mathrm{d}u \tag{A.44}$$

$$= \frac{2}{\alpha_3}\tan^{-1}(u) \tag{A.45}$$

$$= \frac{2}{\alpha_3}\tan^{-1}(\mathrm{e}^{\alpha_3(t+k_3)}) \tag{A.46}$$

Therefore

$$\frac{1}{\alpha_2}\ln(\tan(\frac{1}{2}(\alpha_2 f_2(t) + \phi_2))) = \frac{2}{\alpha_3}\tan^{-1}(\mathrm{e}^{\alpha_3(t+k_3)}) \tag{A.47}$$

and so

$$\alpha_2 f_2(t) + \phi_2 = 2\tan^{-1}(\mathrm{e}^{\frac{2\alpha_2}{\alpha_3}(\tan^{-1}(\mathrm{e}^{\alpha_3(t+k_3)}))}) \tag{A.48}$$

# Appendix B

# Integration of Functions in Chapter 4

## B.1 The Torus

In Chapter 4 Section 4.1, a torus, the simplification of the general model resulted in a differential equation for $f_2'(t)$ which was integrated with respect to time $t$ as follows.

$$f_2'(t) = \sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} \tag{B.1}$$

$$= a_1 + a_2 \sin(\alpha_2 f_2(t) + \phi_2) \tag{B.2}$$

from Equation 4.4 on page 87. Therefore

$$\int \frac{\mathrm{d}f_2(t)}{a_1 + a_2 \sin(\alpha_2 f_2(t) + \phi_2)} = \int \mathrm{d}t \tag{B.3}$$

Considering the left hand side of Equation B.3 let $p = \tan(\frac{\alpha_2 f_2(t) + \phi_2}{2})$ and so

$$\int \frac{\mathrm{d}f_2(t)}{a_1 + a_2 \sin(\alpha_2 f_2(t) + \phi_2)} = \frac{1}{\alpha_2} \int \frac{1}{a_1 + a_2 \frac{2p}{1+p^2}} \frac{2\mathrm{d}p}{1+p^2} \tag{B.4}$$

$$= \frac{2}{\alpha_2 a_1}\int \frac{1}{p^2 + \frac{2a_2}{a_1}p + 1}\mathrm{d}p \tag{B.5}$$

$$= \frac{2}{\alpha_2 a_1}\int \frac{1}{(p + \frac{a_2}{a_1})^2 + (\sqrt{1 - \frac{a_2^2}{a_1^2}})^2}\mathrm{d}p \tag{B.6}$$

$$= \frac{2}{\alpha_2 a_1\sqrt{1 - \frac{a_2^2}{a_1^2}}}\int \frac{\sqrt{1 - \frac{a_2^2}{a_1^2}}}{(p + \frac{a_2}{a_1})^2 + (\sqrt{1 - \frac{a_2^2}{a_1^2}})^2}\mathrm{d}p \tag{B.7}$$

$$= \frac{2}{\alpha_2 a_1\sqrt{1 - \frac{a_2^2}{a_1^2}}}\tan^{-1}(\frac{p + \frac{a_2}{a_1}}{\sqrt{1 - \frac{a_2^2}{a_1^2}}}) \tag{B.8}$$

$$= \frac{2}{\alpha_2\sqrt{a_1^2 - a_2^2}}\tan^{-1}(\frac{a_1 p + a_2}{\sqrt{a_1^2 - a_2^2}}) \tag{B.9}$$

$$= \frac{2}{\alpha_2\sqrt{a_1^2 - a_2^2}}\tan^{-1}(\frac{a_1\tan(\frac{1}{2}(\alpha_2 f_2(t) + \phi_2) + a_2}{\sqrt{a_1^2 - a_2^2}}) \tag{B.10}$$

Integrating the right hand side of Equation B.3 gives

$$\int \mathrm{d}t = t + k_1 \tag{B.11}$$

where $k_1$ is the constant of integration. Therefore Equation B.3 integrates to

$$\alpha_2 f_2(t) + \phi_2 = 2\tan^{-1}\Big[\frac{\sqrt{a_1^2 - a_2^2}}{a_1}\tan[\frac{1}{2}\alpha_2\sqrt{a_1^2 - a_2^2}(t + k_1)] - a_2\Big] \tag{B.12}$$

## Model 2

In this model the choice of $f_1'(t)$ was such that

$$\begin{aligned}
\frac{\mathrm{d}f_1(t)}{\mathrm{d}t} &= (x_1 - x_1^*)(x_2 - x_2^*) &\text{(B.13)}\\
&= (a_1 + a_2\sin(\alpha_2 f_2(t) + \phi_2))^2\cos(\alpha_1 f_1(t) + \phi_1)\sin(\alpha_1 f_1(t) + \phi_1) &\text{(B.14)}
\end{aligned}$$

from Equations 4.4 and so

$$\int \frac{\mathrm{d}f_1(t)}{\cos(\alpha_1 f_1(t)+\phi_1)\sin(\alpha_1 f_1(t)+\phi_1)} = \int (a_1 + a_2 \sin(\alpha_2 f_2(t)+\phi_2))^2 \mathrm{d}t \qquad \text{(B.15)}$$

The left hand side of Equation B.15 can be integrated in the same way as the left hand side of Equation A.11 to give

$$\int \frac{\mathrm{d}f_1(t)}{\cos(\alpha_1 f_1(t)+\phi_1)\sin(\alpha_1 f_1(t)+\phi_1)} = \frac{1}{\alpha_1}\ln(\frac{1}{2}\tan(\alpha_1 f_1(t)+\phi_1)) \qquad \text{(B.16)}$$

It can be noted that

$$\frac{\mathrm{d}f_2(t)}{\mathrm{d}t} = a_1 + a_2 \sin(\alpha_2 f_2(t)+\phi_2) \qquad \text{(B.17)}$$

from Equation B.3 and so the right hand side of Equation B.15 becomes

$$\int (a_1 + a_2 \sin(\alpha_2 f_2(t)+\phi_2))^2 \mathrm{d}t = \int (a_1 + a_2 \sin(\alpha_2 f_2(t)+\phi_2)) \mathrm{d}f_2(t) \qquad \text{(B.18)}$$

$$= \frac{1}{\alpha_2}(a_1(\alpha_2 f_2(t)+\phi_2) - a_2\cos(\alpha_2 f_2(t)+\phi_2)) \qquad \text{(B.19)}$$

Therefore

$$\frac{1}{\alpha_1}\ln(\frac{1}{2}\tan(\alpha_1 f_1(t)+\phi_1) = \frac{1}{\alpha_2}(a_1(\alpha_2 f_2(t)+\phi_2) - a_2\cos(\alpha_2 f_2(t)+\phi_2)) \qquad \text{(B.20)}$$

and so

$$\alpha_1 f_1(t)+\phi_1 = \tan^{-1}(2e^{\frac{\alpha_1}{\alpha_2}(a_1(\alpha_2 f_2(t)+\phi_2) - a_2\cos(\alpha_2 f_2(t)+\phi_2)}) \qquad \text{(B.21)}$$

where $\alpha_2 f_2(t)+\phi_2 = 2\tan^{-1}\frac{1}{a_1}\left[\sqrt{a_1^2-a_2^2}\tan[\frac{1}{2}\alpha_2\sqrt{a_1^2-a_2^2}(t+k_1)] - a_2\right]$.

## B.2 Four–dimensional Torus

In this set of models the functions $f_2(t)$ and $f_3(t)$ can be found from the integration done previously.

$$f_3'(t) = \sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2 + (x_3 - x_3^*)^2} \tag{B.22}$$

$$= a_1 + a_2 \sin(\alpha_3 f_3(t) + \phi_3) \tag{B.23}$$

This is exactly the same as that for $f_2(t)$ in the three–dimensional torus and so

$$\alpha_3 f_3(t) + \phi_3 = 2\tan^{-1}\Big[\frac{\sqrt{a_1^2 - a_2^2}}{a_1}\tan[\frac{1}{2}\alpha_3\sqrt{a_1^2 - a_2^2}(t + k_3)] - a_2\Big] \tag{B.24}$$

An expression for $f_2(t)$ can be found as follows:

$$f_3'(t) = \sqrt{(x_1 - x_1^*)^2 + (x_2 - x_2^*)^2} \tag{B.25}$$

$$= (a_1 + a_2 \sin(\alpha_3 f_3(t) + \phi_3)) \sin(\alpha_2 f_2(t) + \phi_2) \tag{B.26}$$

and so

$$\int \frac{\mathrm{d}f_2(t)}{\sin(\alpha_2 f_2(t) + \phi_2)} = \int a_1 + a_2 \sin(\alpha_3 f_3 + \phi_3)\mathrm{d}t \tag{B.27}$$

$$\frac{1}{\alpha_2}\ln(\tan(\frac{\alpha_2 f_2(t) + \phi_2}{2})) = \int a_1 + a_2 \sin(\alpha_3 f_3 + \phi_3)\mathrm{d}t. \tag{B.28}$$

Now

$$\frac{\mathrm{d}f_3(t)}{\mathrm{d}t} = a_1 + a_2 \sin(\alpha_3 f_3(t) + \phi_3) \tag{B.29}$$

and so the right hand side of Equation B.28 is simply

$$\int \mathrm{d}f_3 = f_3 + k. \tag{B.30}$$

Using the notation $\theta_3 = \alpha_3 f_3(t) + \phi_3$ it can be found that

$$\alpha_2 f_2 + \phi_2 = 2\tan^{-1}\left[\exp[\frac{\alpha_2}{\alpha_3}\theta_3 + k_2]\right] \tag{B.31}$$

# Appendix C

# Computer Programs

## C.1 Fixed Points and Eigenvalues

```
C----------------------------------------------------------------------------
C     THIS PROGRAM FIRSTLY FINDS THE FIXED POINTS  OF N NON LINEAR EQUATIONS
C     IN N  UNKNOWNS. IT THEN GOES ON TO FIND THE EIGENVALUES OF THE
C     JACOBIAN  MATRIX OF THE N DIFFERENTAL EQUATIONS EVALUATED AT THE
C     FIXED POINTS. THE  EIGENVALUES ARE RETURNED IN THE FORM (A,B) WHERE A
C     IS THE REAL PART AND B IS THE IMAGINARY PART.
C----------------------------------------------------------------------------
      PROGRAM FIXEIEGEN
      INTEGER IFAIL,J,N, LWA
C-----------------------------------------------
C     N SPECIFIES THE NUMBER OF EQUATIONS
C-----------------------------------------------
      PARAMETER  (N=2,LWA=(N*(3*N+13))/2)
      DOUBLE PRECISION FNORM, TOL,FVEC(N),WA(LWA)
      DOUBLE PRECISION X(N),F05ABF,X02AAF
      EXTERNAL C05NBF,F05ABF, X02AAF,FCN
      INTEGER  I,NMAX, IA
      PARAMETER      (NMAX=N,IA=NMAX)
      INTEGER INTGER(NMAX)
      DOUBLE PRECISION A(IA,NMAX), RI(NMAX), RR(NMAX)
      DOUBLE PRECISION ALPHA1,ALPHA2,B,X0,Y0,Z0,E,F,G,H,O
      EXTERNAL      F02AFF
      INTRINSIC  SQRT
C----------------------------------------------------------------
C     THE FOLLOWING STARTING VALUES PROVIDE A ROUGH SOLUTION
C     FOR THE FIXED POINT
C----------------------------------------------------------------
      X(J)= 0.000
      TOL = SQRT(X02AAF(0.0D0))
      IFAIL = 0
      CALL C05NBF(FCN,N,X,FVEC,TOL,WA,LWA,IFAIL)
      FNORM = F05ABF(FVEC,N)
      WRITE(*,FMT=101) (X(J),J=1,N)
 101  FORMAT('FIXED POINT'/ ,3F13.5)
```

```
C-----------------------------------------------------------------------
C   TRANSFERING THE FIXED POINTS INTO THE EIGENVALUE ROUTINE
C-----------------------------------------------------------------------
      W=X(1)
      Y=X(2)
      Z=X(3)
C-----------------------------------------------------------------------
C     FORMULATION OF THE JACOBIAN MATRIX.
C     A(i,j) CONTAINS d/dxj(dxi/dt) EVALUATED AT THE FIXED POINTS
C     OF THE SYSTEM OF DIFFERENTIAL EQUATIONS
C-----------------------------------------------------------------------

C     PREDITOR PREY

      A1=1.0
      A2=0.5
      B1=0.004
      B2=0.08
      C1=0.1
      C2=0.05
      A(1,1)=-B1*W
      A(1,2)=-C1*Y
      A(2,1)=C2*W
      A(2,2)=-B2*Y

      CALL F02AFF(A,IA,N,RR,RI,INTGER,IFAIL)
     WRITE (*,FMT=100) (RR(I),RI(I),I=1,N)
      STOP

 100  FORMAT (' EIGENVALUES',/(' (',F7.3,',',F7.3,')'))
      END

C-----------------------------------------------------------------------
C     THIS SUBROUTINE CONTAINS THE N NON LINEAR EQUATIONS.THEY
C     MUST BE WRITTEN IN THE FORM FVEC(N)=FUNCTION(X(1),X(2)...)
C     WHERE FVEC(N)=0.
C-----------------------------------------------------------------------
      SUBROUTINE FCN(N,X,FVEC,IFLAG)
      INTEGER  IFLAG, N
      DOUBLE PRECISION FVEC(N), X(N)
      DOUBLE PRECISION ALPHA1,ALPHA2,B,X0,Y0,Z0,E,F,G,H,O

C     PREDITOR PREY
      D1=1.0
      D2=0.5
      B1=0.004
      B2=0.08
      C1=0.1
      C2=0.05
      FVEC(1)=D1-B1*X(1)-C1*X(2)
      FVEC(2)=D2-B2*X(2)+C2*X(3)
      RETURN
      END
```

# C.2 Integrating Differential Equations

Below is the listing for the program which solves the differential equations. It is only shown for the three dimensional ellipsoid. The same basic program is easily adapted for the other situations.

```
C---------------------------------------------------------------------------
C     THIS IS A PROGRAM WHICH SOLVES N FIRST ORDER DIFFERENTIAL EQUATIONS
C     OVER  A GIVEN RANGE AND PRINTS THE SOLUTIONS AT SPECIFIED INTEVALS.
C---------------------------------------------------------------------------
      PROGRAM RUNGE
C---------------------------------------------------------------------------
C     N SPECIFIES THE NUMBER OF DIFFERENTIAL EQUATIONS IN THE SET
C---------------------------------------------------------------------------
      PARAMETER (N=3)
      IMPLICIT REAL*8(A-H,O-Z)
      IMPLICIT INTEGER*4(I-N)
      DOUBLE PRECISION W(N,1000),Y(N)
      INTRINSIC DBLE
      EXTERNAL D02BBF,FCN,OUT
      COMMON XEND,H,I
C---------------------------------------------------------------------------
C     THE OUTPUT IS SAVED IN  FILES WHICH WILL EACH CONTAIN THE INDEPENDENT
C     VARIABLE EG TIME AND THE CORRESPONDING DEPENDENT VARIABLE
C---------------------------------------------------------------------------
      OPEN(11,FILE='DATAX1.DAT',STATUS='UNKNOWN')
      OPEN(12,FILE='DATAX2.DAT',STATUS='UNKNOWN')
      OPEN(13,FILE='DATAX3.DAT',STATUS='UNKNOWN')
C---------------------------------------------------------------------------
C     XEND SPECIFIES THE LAST VALUE OF THE INDEPENDENT VARIABLE IE TIME ETC.
C     XEND=100 MEANS THE PROCESS CONTINUES UNTILL TIME =100.      |
C---------------------------------------------------------------------------
      IR=0
      XEND=200
      TOL=10.0D0**(-12)
      X= 0.00D0
C------------------------------------------
C     INITIAL VALUES OF X1,X2,X3 ETC
C------------------------------------------
C---------------------------------------------------------------------------
C INITIAL VALUES FOR ELLIPSOID. GIVE IT X1 AND X2 AND IT WORKS OUT X3
C FOR THAT PARTICULAR ELLIPSOID. SO ALSO NEED TO GIVE IT A,B,C,X1F,X2F,X3F
C---------------------------------------------------------------------------
      A1=10.0D0
      A2=20.0D0
      A3=40.0D0
      X1F=15.0D0
      X2F=25.0D0
      X3F=45.0D0
      Y(1)= 6.0D0
      Y(2)=26.0D0
      RX1=Y(1)-X1F
      RX2=Y(2)-X2F
      Y(3)=SQRT(A3**2*(1-((RX1**2)/(A1**2))-((RX2**2)/(A2**2))))+X3F
C     Y(3)=-SQRT(A3**2*(1-((RX1**2)/(A1**2))-((RX2**2)/(A2**2))))+X3F
C---------------------------------------------------------------------------
C     I SETS THE NUMBER OF STEP YOU REQUIRE TO BE PRINTED OUT. NOTE IT SHOUD
C     BE ONE LESS THAN THE NUMBER REQUIRED. IE X=99 100 STEPS WOULD BE
C     PRINTED
C---------------------------------------------------------------------------
      I= 399
      H=(XEND-X)/DBLE(I+1)
      IFAIL=-1
```

```
      CALL D02BBF(X,XEND,N,Y,TOL,IR,FCN,OUT,W,IFAIL)
      IF (TOL.LT.0.0D0) WRITE(*,FMT=100)
      STOP
 100  FORMAT('RANGE TOO SHORT FOR TOL')
      END
C-----------------------------------------------------------------------
C     THIS SUBROUTINE CONTAINS THE EQUATIONS. THEY MUST BE WRITTEN IN THE
C     FORM F(N)=FUNCTION(Y(N)) IE F(1)=dX1/dt FOR EXAMPLE AND Y(1)=X1, Y(2)=X2 ETC
C-----------------------------------------------------------------------
      SUBROUTINE FCN(T,Y,F)
      IMPLICIT REAL*8(A-H,O-Z)
      IMPLICIT INTEGER*4(I-N)
      PARAMETER (N=3)
      DOUBLE PRECISION F(N),Y(N)
C     3 VARIABLE ELLIPSOID
      A1=10.0D0
      A2=20.0D0
      A3= 40.0D0
      ALPHA1=0.200d0
      ALPHA2=0.032d0
      X1F=15.0D0
      X2F=25.0D0
      X3F=45.0D0
      RX1=Y(1)-X1F
      RX2=Y(2)-X2F
      RX3=Y(3)-X3F
      G=((RX1**2)/(A1**2))+((RX2**2)/(A2**2))
      F1DASH=1
C     F1DASH=RX1*RX2
C     F1DASH=RX1+RX2
      F(1)=(ALPHA2*F3*RX1*RX3)/(A3)-(A1*ALPHA1/A2)*RX2*F1DASH
      F(2)=(ALPHA2*F3*RX2*RX3)/(A3)+(A2*ALPHA1/A1)*RX1*F1DASH
      F(3)=-A3*ALPHA2*G*F3
      RETURN
      END
C-----------------------------------------------------------------------
C     THIS SUBROUTINE SPECIFIES HOW MANY AND HOW OFTEN THE SOLUTIONS ARE
C     PRINTED. CONTROLED BY I AND XEND IN MAIN PROGRAM.
C-----------------------------------------------------------------------
      SUBROUTINE OUT(X,Y)
      IMPLICIT REAL*8(A-H,O-Z)
      IMPLICIT INTEGER*4(I-N)
      PARAMETER (N=3)
      DOUBLE PRECISION Y(N)
      INTRINSIC DBLE
      COMMON XEND,H,I
      WRITE (11,101) X,Y(1)
      WRITE (12,101) X,Y(2)
      WRITE (13,101) X,Y(3)
      X=XEND-DBLE(I)*H
      I=I-1
      RETURN
 101  FORMAT(F13.5,' , ',F13.5)
 103  FORMAT(F13.5,' , ',F13.5,' , ',F13.5,' , ',F13.5)
      END
```

## C.3 The NAG Routines

The following pages are copies of the information about the three NAG routines used in the preceding programs.

# C05NBF – NAG FORTRAN Library Routine Document

NOTE: before using this routine, please read the appropriate implementation document to check the interpretation of ***bold italicised*** terms and other implementation–dependent details. The routine name may be precision–dependent.

## 1. Purpose

C05NBF is an easy-to-use routine to find a zero of a system of N nonlinear functions in N variables by a modification of the Powell hybrid method.

## 2. Specification

```
      SUBROUTINE C05NBF (FCN, N, X, FVEC, XTOL, WA, LWA, IFAIL)
C     INTEGER N, LWA, IFAIL
C     real X(N), FVEC(N), XTOL, WA(LWA)
C     EXTERNAL FCN
```

## 3. Description

C05NBF is based upon the MINPACK routine HYBRD1. It chooses the correction at each step as a convex combination of the Newton and scaled gradient directions. Under reasonable conditions this guarantees global convergence for starting points far from the solution and a fast rate of convergence. The Jacobian is updated by the rank–1 method of Broyden. At the starting point the Jacobian is approximated by forward differences, but these are not used again until the rank–1 method fails to produce satisfactory progress.

## 4. References

[1] POWELL, M.J.D.
A hybrid method for nonlinear algebraic equations. In 'Numerical Methods for Nonlinear Algebraic Equations', Ed. Rabinowitz, P., Gordon and Breach, 1970.

[2] MORE, J.J., GARBOW, B.S. and HILLSTROM, K.E.
User Guide for MINPACK–1.
ANL–80–74, Argonne National Laboratory.

## 5. Parameters

FCN – SUBROUTINE, supplied by the user.

FCN must calculate the values of the functions at X and return these in the vector FVEC.
Its specification is:–

```
SUBROUTINE FCN(N,X,FVEC,IFLAG)
INTEGER N,IFLAG
real X(N),FVEC(N)
```

N – INTEGER.

On entry, N contains the number of equations.
The value of N must not be changed by FCN.

X – ***real*** array of DIMENSION (N).

On entry, X contains the point at which the functions are to be evaluated.
The values in X must not be changed by FCN.

FVEC – *real* array of DIMENSION (N).

On exit, unless IFLAG is reset to a negative number, FVEC(i) must contain the value of the (i)th function evaluated at X.

IFLAG – INTEGER.

In general, IFLAG should not be reset by FCN. If, however, the user wishes to terminate execution (perhaps because some illegal point X has been reached) then IFLAG should be set to a negative integer. This value will be returned through IFAIL.

FCN must be declared as EXTERNAL in the calling (sub)program.

N – INTEGER.

On entry, N must specify the number of equations.
$N > 0$.

Unchanged on exit.

X – *real* array of DIMENSION at least (N).

Before entry, X(j) must be set to a guess at the j(th) component of the solution (j = 1,2,...,N).

On exit, X contains the final estimate of the solution vector.

FVEC – *real* array of DIMENSION at least (N).

On exit, FVEC contains the function values at the final point, X.

XTOL – *real*.

On entry, XTOL must specify the accuracy in X to which the solution is required.
$XTOL \geq 0.0$. The recommended value is the square root of machine precision.

Unchanged on exit.

WA – *real* array of DIMENSION at least (LWA).

Used as workspace.

LWA – INTEGER.

On entry, LWA must specify the dimension of the array WA.
$LWA \geq \frac{1}{2} N \times (3 \times N + 13)$.

Unchanged on exit.

IFAIL – INTEGER.

On entry, IFAIL must be set to 0 or 1. For users not familiar with this parameter (described in Chapter P01) the recommended value is 0.

Unless the routine detects an error (see next section), IFAIL contains 0 on exit.

## 6. Error Indicators and Warnings

Errors detected by the routine:–

IFAIL < 0

This indicates an exit from C05NBF because the user has set IFLAG negative in FCN. The value of IFAIL will be the same as the user's setting of IFLAG.

IFAIL = 1

On entry, $N \leq 0$,
or $XTOL < 0.0$,
or $LWA < \frac{1}{2}N \times (3 \times N + 13)$.

IFAIL = 2

There have been at least $200 \times (N+1)$ evaluations of FCN. Consider restarting the calculation from the final point held in X.

IFAIL = 3

No further improvement in the approximate solution X is possible; XTOL is too small.

IFAIL = 4

The iteration is not making good progress. This failure exit may indicate that the system does not have a zero, or that the solution is very close to the origin (see Section 10). Otherwise, rerunning C05NBF from a different starting point may avoid the region of difficulty. Alternatively consider using C05PBF or C05PCF which require an analytic Jacobian.

## 7. Auxiliary Routines

Details are distributed to sites in machine-readable form.

## 8. Timing

The time required by C05NBF to solve a given problem depends on N, the behaviour of the functions, the accuracy requested and the starting point. The number of arithmetic operations executed by C05NBF to process each call of FCN is about $11.5 \times N^2$. Unless FCN can be evaluated quickly, the timing of C05NBF will be strongly influenced by the time spent in FCN.

## 9. Storage

There are no internally declared arrays.

## 10. Accuracy

C05NBF tries to ensure that

$$||X - XSOL||_2 \leq XTOL \times ||XSOL||_2.$$

If this condition is satisfied with $XTOL = 10^{-k}$ then the larger components of X have k significant decimal digits. There is a danger that the smaller components of X may have large relative errors, but the fast rate of convergence of C05NBF usually avoids this possibility.

If XTOL is less than machine precision (see NAG Library routine X02AAF), and the above test is satisfied with the machine precision in place of XTOL, then the routine exits with IFAIL = 3.

Note that this convergence test is based purely on relative error, and may not indicate convergence if the solution is very close to the origin.

The test assumes that the functions are reasonably well behaved. If this condition is not satisfied, then C05NBF may incorrectly indicate convergence. The validity of the answer can be checked, for example, by rerunning C05NBF with a tighter tolerance.

## 11. Further Comments

Ideally the problem should be scaled so that at the solution the function values are of comparable magnitude.

## 12. Keywords

Equations, nonlinear algebraic, easy-to-use;
Powell Hybrid Method, easy-to-use.

## 13. Example

To determine the values $x_1,...,x_9$ which satisfy the tridiagonal equations:–

$$(3-2x_1)x_1 - 2x_2 = -1$$

$$-x_{i-1} + (3-2x_i)x_i - 2x_{i+1} = -1, \quad i = 2,3,...,8$$

$$-x_8 + (3-2x_9)x_9 = -1$$

### 13.1. Program Text

WARNING: This single precision example program may require amendment for certain implementations. The results produced may not be the same. If in doubt, please seek further advice (see Essential Introduction to the Library Manual).

```
C      C05NBF EXAMPLE PROGRAM TEXT
C      MARK 9 RELEASE. NAG COPYRIGHT 1981
C      .. LOCAL SCALARS ..
       REAL FNORM, TOL
       INTEGER IFAIL, J, NOUT
C      .. LOCAL ARRAYS ..
       REAL FVEC(9), WA(180), X(9)
C      .. FUNCTION REFERENCES ..
       REAL F05ABF, SQRT, X02AAF
C      .. SUBROUTINE REFERENCES ..
C      C05NBF
C      ..
       EXTERNAL FCN
       DATA NOUT /6/
       WRITE (NOUT,99999)
C      THE FOLLOWING STARTING VALUES PROVIDE A ROUGH SOLUTION.
       DO 20 J=1,9
          X(J) = -1.E0
    20 CONTINUE
       TOL = SQRT(X02AAF(0.0))
       IFAIL = 0
       CALL C05NBF(FCN, 9, X, FVEC, TOL, WA, 180, IFAIL)
       FNORM = F05ABF(FVEC,9)
       WRITE (NOUT,99998) FNORM, IFAIL, (X(J),J=1,9)
       STOP
99999 FORMAT (4(1X/), 31H C05NBF EXAMPLE PROGRAM RESULTS/1X)
99998 FORMAT (5X, 31H FINAL L2 NORM OF THE RESIDUALS, E12.4//5X,
     * 15H EXIT PARAMETER, I10//5X, 27H FINAL APPROXIMATE SOLUTION//
     * (5X, 3E12.4))
       END
       SUBROUTINE FCN(N, X, FVEC, IFLAG)
C      .. SCALAR ARGUMENTS ..
       INTEGER IFLAG, N
C      .. ARRAY ARGUMENTS ..
       REAL FVEC(N), X(N)
C      ..
C      .. LOCAL SCALARS ..
       REAL ONE, TEMP, TEMP1, TEMP2, THREE, TWO, ZERO
       INTEGER K
C      ..
       DATA ZERO, ONE, TWO, THREE /0.E0,1.E0,2.E0,3.E0/
```

```
      DO 20 K=1,N
         TEMP = (THREE-TWO*X(K))*X(K)
         TEMP1 = ZERO
         IF (K.NE.1) TEMP1 = X(K-1)
         TEMP2 = ZERO
         IF (K.NE.N) TEMP2 = X(K+1)
         FVEC(K) = TEMP - TEMP1 - TWO*TEMP2 + ONE
   20 CONTINUE
      RETURN
      END
```

### 13.2. Program Data

None.

### 13.3. Program Results

```
 C05NBF EXAMPLE PROGRAM RESULTS

      FINAL L2 NORM OF THE RESIDUALS  0.1193E-07

      EXIT PARAMETER          0

      FINAL APPROXIMATE SOLUTION

      -0.5707E+00 -0.6816E+00 -0.7017E+00
      -0.7042E+00 -0.7014E+00 -0.6919E+00
      -0.6658E+00 -0.5960E+00 -0.4164E+00
```

1. Purpose

F02AFF calculates all the eigenvalues of a real unsymmetric matrix by reduction to Hessenberg form and the QR algorithm.

IMPORTANT: before using this routine, read the appropriate machine implementation document to check the interpretation of italicised terms and other implementation-dependent details.

2. Specification (FORTRAN IV)

```
      SUBROUTINE F02AFF(A,IA,N,RR,RI,INTGER,IFAIL)
C     INTEGER IA,N,INTGER(N),IFAIL
C     real A(IA,N),RR(N),RI(N)
```

3. Description

The matrix is first reduced to upper Hessenberg form using stabilised elementary similarity transformations with *additional precision* accumulation of innerproducts. The eigenvalues are then found using the QR algorithm for real Hessenberg matrices.

4. References

[1] WILKINSON, J.H. and REINSCH, C.
Handbook for Automatic Computation.
Volume II, Linear Algebra, pp. 339-358 and 359-371,
Springer-Verlag, 1971.

5. Parameters

A - *real* array of DIMENSION (IA,s) where s ≥ N.
Before entry, A must contain the elements of the matrix.
On exit, the array is overwritten.

IA - INTEGER.
On entry, IA specifies the first dimension of array A as declared in the calling (sub)program. IA ≥ N.
Unchanged on exit.

N - INTEGER.
On entry, N specifies the order of the matrix.
Unchanged on exit.

RR, RI - *real* arrays of DIMENSION at least (N).
On successful exit, RR contains the real parts and RI the imaginary parts of the eigenvalues.

5. Parameters (contd)

INTGER - INTEGER array of DIMENSION at least (N).
Used as working space. On successful exit, INTGER contains the number of iterations for each eigenvalue. If two eigenvalues are found simultaneously then the number of iterations is given with a positive sign for the first of the pair and with a negative sign for the second.

IFAIL - INTEGER.
Before entry, IFAIL must be assigned a value. For users not familiar with this parameter (described in Chapter P01) the recommended value is 0. Unless the routine detects an error (see Section 6), IFAIL contains 0 on exit.

6. Error Indicators

Errors detected by the routine:-

IFAIL = 1 More than 30 * N iterations are required to isolate all the eigenvalues.

7. Auxiliary Routines

This routine calls the NAG Library routines F01AKF, F02APF, P01AAF and X02AAF.

8. Timing

The time taken is approximately proportional to $N^3$.

9. Storage

There are no internally declared arrays.

10. Accuracy

The accuracy of the results depends on the original matrix and the multiplicity of the roots. For a detailed error analysis see [1], pages 352 and 367.

11. Further Comments None.

12. Keywords

Eigenvalues.
QR Algorithm.
Real Matrix.
Stabilised Elementary Similarity Transformations.

## 13. Example

To calculate all the eigenvalues of the real matrix:

$$\begin{pmatrix} 4 & -5 & 0 & 3 \\ 0 & 4 & -3 & -5 \\ 5 & -3 & 4 & 0 \\ 3 & 0 & 5 & 4 \end{pmatrix}$$

### Program

This single precision example program may require amendment
 i) for use in a DOUBLE PRECISION implementation
ii) for use in either precision in certain implementations.
The results produced may differ slightly.

```
C     F02AFF EXAMPLE PROGRAM TEXT
C     NAG COPYRIGHT 1975
C     MARK 4.5 REVISED
C
      REAL A(5,5), RR(5), RI(5), TITLE(7)
      INTEGER NIN, NOUT, I, N, J, IA, IFAIL, INTGER(5)
      DATA NIN /5/, NOUT /6/
      READ (NIN,99999) (TITLE(I),I=1,7)
      WRITE (NOUT,99997) (TITLE(I),I=1,6)
      N = 4
      READ (NIN,99998) ((A(I,J),J=1,N),I=1,N)
      IA = 5
      IFAIL = 1
      CALL F02AFF(A, IA, N, RR, RI, INTGER, IFAIL)
      IF (IFAIL.EQ.0) GO TO 20
      WRITE (NOUT,99996) IFAIL
      STOP
   20 WRITE (NOUT,99995) (RR(I),RI(I),I=1,N)
      STOP
99999 FORMAT (6A4, 1A3)
99998 FORMAT (4F5.0)
99997 FORMAT (4(1X/), 1H , 5A4, 1A3, 7HRESULTS/1X)
99996 FORMAT (25H0ERROR IN F02AFF IFAIL = , I2)
99995 FORMAT (12H0EIGENVALUES/(2H (, F5.2, 1H,, F5.2, 1H)))
      END
```

13. Example (contd)

Data

```
F02AFF EXAMPLE PROGRAM DATA
     4   -5    0    3
     0    4   -3   -5
     5   -3    4    0
     3    0    5    4
```

Results

```
F02AFF EXAMPLE PROGRAM RESULTS

EIGENVALUES
(12.00, 0.00)
( 1.00, 5.00)
( 1.00,-5.00)
( 2.00, 0.00)
```

# D02BBF – NAG FORTRAN Library Routine Document

NOTE: before using this routine, please read the appropriate implementation document to check the interpretation of ***bold italicised*** terms and other implementation-dependent details. The routine name may be precision-dependent.

## 1. Purpose

D02BBF integrates a system of first-order ordinary differential equations over a range with suitable initial conditions, using a Runge–Kutta–Merson method, and returns the solution at points specified by the user.

## 2. Specification

```
      SUBROUTINE D02BBF (X, XEND, N, Y, TOL, IRELAB, FCN, OUTPUT,
     1   W, IFAIL)
C     INTEGER N, IRELAB, IFAIL
C     real X, XEND, Y(N), TOL, W(N,7)
C     EXTERNAL FCN, OUTPUT
```

## 3. Description

The routine integrates a system of ordinary differential equations

$$Y_i' = F_i(T,Y_1,Y_2,...,Y_N), \qquad i = 1,2,...,N,$$

from T = X to T = XEND using a Merson form of the Runge–Kutta method. The system is defined by a subroutine FCN supplied by the user, which evaluates $F_i$ in terms of T and $Y_1,Y_2,...,Y_N$ (see Section 5), and the values of $Y_1,Y_2,...,Y_N$ must be given at T = X.

The solution is returned via the user supplied routine OUTPUT at a set of points specified by the user. This solution is obtained by quintic Hermite interpolation on solution values produced by the Runge–Kutta method.

The accuracy of the integration and, indirectly, the interpolation is controlled by the parameters TOL and IRELAB.

For a description of Runge–Kutta methods and their practical implementation see [1].

## 4. References

[1] HALL, G and WATT, J.M. (eds.)
Modern Numerical Methods for Ordinary Differential Equations, p. 59.
Clarendon Press, Oxford, 1976.

## 5. Parameters

X – *real*.

Before entry, X must be set to the initial value of the independent variable T.

On exit, it contains XEND, unless an error has occurred, when it contains the value of T at the error.

XEND – *real*.

On entry, XEND must specify the final value of the independent variable. If XEND < X on entry, integration will proceed in a negative direction.

Unchanged on exit.

N – INTEGER.

On entry, N must specify the number of differential equations.

Unchanged on exit.

Y – *real* array of DIMENSION at least (N).

Before entry, Y(1),Y(2),...,Y(N) must contain the initial values of the solution $Y_1,Y_2,...,Y_N$.

On exit, Y(1),Y(2),...,Y(N) contain the computed values of the solution at the final value of T.

TOL – *real*.

Before entry, TOL must be set to a positive tolerance for controlling the error in the integration. The routine D02BBF has been designed so that, for most problems, a reduction in TOL leads to an approximately proportional reduction in the error in the solution at XEND. The relation between changes in TOL and the error at intermediate output points is less clear, but for TOL small enough the error at intermediate output points should also be approximately proportional to TOL. However, the actual relation between TOL and the accuracy achieved cannot be guaranteed. The user is strongly recommended to call D02BBF with more than one value for TOL and to compare the results obtained to estimate their accuracy. In the absence of any prior knowledge, the user might compare the results obtained by calling D02BBF with TOL = $10.0^{-P}$ and TOL = $10.0^{-P-1}$ when P correct decimal digits are required in the solution.

TOL is normally unchanged on exit. However if the range X to XEND is so short that a small change in TOL is unlikely to make any change in the computed solution then, on return, TOL has its sign changed. This should be treated as a warning that the computed solution is likely to be more accurate than would be produced by using the same value of TOL on a longer range of integration.

IRELAB – INTEGER.

On entry, IRELAB must determine the type of error control. At each step in the numerical solution an estimate of the local error, EST, is made. For the current step to be accepted the following condition must be satisfied:

IRELAB = 0

$EST \le TOL \times \max\{1.0, |Y(1)|, |Y(2)|, \ldots, |Y(N)|\};$

IRELAB = 1

$EST \le TOL;$

IRELAB = 2

$EST \le TOL \times \max\{eps, |Y(1)|, |Y(2)|, \ldots, |Y(N)|\},$

Where eps is a small machine-dependent number.

If the appropriate condition is not satisfied, the stepsize is reduced and the solution is recomputed on the current step.

If the user wishes to measure the error in the computed solution in terms of the number of correct decimal places, then IRELAB should be given the value 1 on entry, whereas if the error requirement is in terms of the number of correct significant digits, then IRELAB should be given the value 2. Where there is no preference in the choice of error test IRELAB = 0 will result in a mixed error test.

Unchanged on exit.

FCN – SUBROUTINE, supplied by the user.

FCN must evaluate the functions $F_i$ (i.e. the derivatives $Y_i'$) for given values of its arguments $T, Y_1, \ldots, Y_N$.

It specification is:

```
SUBROUTINE FCN(T,Y,F)
real T,Y(n),F(n)
```

where n is the actual value of N in the call of D02BBF.

T – *real*.

On entry, T specifies the value of the argument T.
Its value must not be changed.

Y – *real* array of DIMENSION (n).

On entry, Y(I) contains the value of the argument $Y_I$, for I = 1,...,n.

These values must not be changed.

F – *real* array of DIMENSION (n).

On exit, F(I) must contain the value of $F_I$, for I = 1,...,n.

FCN must be declared as EXTERNAL in the (sub)program from which D02BBF is called.

OUTPUT – SUBROUTINE, supplied by the user.

OUTPUT allows the user to have access to intermediate values of the computed solution (e.g. to print or plot them), at successive points specified by the user. It is initially called by D02BBF with XSOL = X (the initial value of T). The user must reset XSOL to the next point where OUTPUT is to be called, and so on at each call to OUTPUT. If, after a call to OUTPUT, the reset point XSOL is beyond XEND, D02BBF will integrate to XEND with no further calls to OUTPUT; if a call to OUTPUT is required at the point XSOL = XEND, then XSOL must be given precisely the value XEND.

The specification of OUTPUT is:

```
SUBROUTINE OUTPUT(XSOL,Y)
real XSOL,Y(n)
```

where n is the actual value of N in the call of D02BBF.

XSOL – *real*.

On entry, XSOL contains the current value of the independent variable T.

On exit, XSOL must contain the next value of T at which OUTPUT is to be called.

Y – *real* array of DIMENSION (n).

On entry, Y contains the computed solution at the point XSOL.
Its elements must not be changed.

OUTPUT must be declared as EXTERNAL in the (sub)program from which D02BBF is called.

W – *real* array of DIMENSION (N,p), where $p \ge 7$.

Used as working space.

IFAIL – INTEGER.

On entry, IFAIL must be set to 0 or 1. For users not familiar with this parameter (described in Chapter P01) the recommended value is 0.

Unless the routine detects an error (see next section), IFAIL contains 0 on exit.

## 6. Error Indicators and Warnings

Errors detected by the routine:–

IFAIL = 1

On entry, TOL $\leq 0$
or N $\leq 0$
or IRELAB$\neq$0, 1 or 2.

IFAIL = 2

With the given value of TOL, no further progress can be made across the integration range from the current point T = X, or the dependence of the error on TOL would be lost if further progress across the integration range were attempted (see Section 11 for a discussion of this error exit). The components Y(1),Y(2),...,Y(N) contain the computed values of the solution at the current point.

IFAIL = 3

TOL is too small for the routine to take an initial step (see Section 11). X and Y(1),Y(2),...,Y(N) retain their initial values.

IFAIL = 4

X = XEND and XSOL$\neq$X after the initial call to OUTPUT.

IFAIL = 5

A value of XSOL returned by OUTPUT lies outside the current range X to XEND and lies closer to X than XEND.

IFAIL = 6

A serious error has occurred in an internal call to D02PAF. Check all subroutine calls and array dimensions. Seek expert help.

IFAIL = 7

A serious error has occurred in an internal call to D02XAF. Check all subroutine calls and array dimensions. Seek expert help.

## 7. Auxiliary Routines

Details are distributed to sites in machine-readable form.

## 8. Timing

This depends on the complexity and mathematical properties of the system of differential equations defined by FCN, on the range, the tolerance and the number of calls to OUTPUT. There is also an overhead of the form A + B $\times$ N where A and B are machine dependent computing times.

## 9. Storage

The storage required by internally declared arrays is 28 ***real*** elements.

## 10. Accuracy

The accuracy depends on TOL, on the mathematical properties of the differential system, on the length of the range of integration and on the method. It can be controlled by varying TOL but the approximate proportionality of the error to TOL holds only for a restricted range of values of TOL. For TOL too large, the underlying theory may break down and the result of varying TOL may be unpredictable. For TOL too small, rounding errors may affect the solution significantly and an error exit with IFAIL = 2 or IFAIL = 3 is possible.

At the intermediate output points the same remarks apply. For large values of TOL it is possible that the errors at some intermediate output points may be much larger than at XEND. In any case, it must not be expected that the error will have the same size at all output points. At any point, it is a combination of the errors arising from the integration of the differential equation and the interpolation. The effect of combining these errors will vary, though in most cases the integration error will dominate.

The user who requires a more reliable estimate of the accuracy achieved than can be obtained by varying TOL, is recommended to call the routine D02BDF where both the solution and a global error estimate are computed.

## 11. Further Comments

If the routine fails with IFAIL = 3, then it can be called again with a larger value of TOL if this has not already been tried. If the accuracy requested is really needed and cannot be obtained with this routine, the system may be very stiff (see below) or so badly scaled that it cannot be solved to the required accuracy.

If the routine fails with IFAIL = 2, it is probable that it has been called with a value of TOL which is so small that the solution cannot be obtained on the range X to XEND. This can happen for well-behaved systems and very small values of TOL. The user should, however, consider whether there is a more fundamental difficulty. For example,

(i) in the region of a singularity (infinite value) of the solution, the routine will usually stop with IFAIL = 2, unless overflow occurs first. If overflow occurs using D02BBF, routine D02PAF can be used instead to trap the increasing solution before overflow occurs. In any case, numerical integration cannot be continued through a singularity, and analytic treatment should be considered;

(ii) for 'stiff' equations where the solution contains rapidly decaying components, the routine will use very small steps in T (internally to D02BBF) to preserve stability. This will exhibit itself by making the computing time excessively long, or occasionally by an exit with IFAIL = 2. Merson's method is not efficient in such cases, and the user should try the Gear method D02EBF. To determine whether a problem is stiff, the routine D02BDF may be used.

For well-behaved systems with no difficulties such as stiffness or singularities, the Merson method should work well for low accuracy calculations (three or four figures). For high accuracy calculations or where FCN is costly to evaluate, Merson's method may not be appropriate and a computationally less expensive method may be the Adams method D02CBF.

Users with problems for which D02BBF is not sufficiently general should consider using the routine D02PAF with routine D02XAF. D02PAF is a more general Merson routine with many facilities including more general error control options and several criteria for interrupting the calculations. Routine D02XAF interpolates on values produced by D02PAF.

## 12. Keywords

Initial Value Problems,
Intermediate Output,
Ordinary Differential Equations,
Runge–Kutta–Merson Method.

## 13. Example

To integrate the following equations (for a projectile)

$$y' = \tan(\phi),$$

$$v' = -0.032\frac{\tan\phi}{v} - 0.02\times v\times\sec(\phi),$$

$$\phi' = -0.032/v^2$$

over an interval X = 0.0, to XEND = 8.0, starting with values y = 0.0, v = 0.5 and $\phi = \pi/5$ and printing the solution at steps of 1.0. We write y = Y(1), v = Y(2) and $\phi$ = Y(3), and we set TOL = 1.0E–4 and TOL = 1.0E–5 in turn so that we may compare the solutions obtained. $\pi$ is calculated using the NAG function X01AAF.

Note the careful construction of routine OUTPUT to ensure that the value at XEND is printed.

### 13.1. Program Text

WARNING: This single precision example program may require amendment for certain implementations. The results produced may not be the same. If in doubt, please seek further advice (see Essential Introduction to the Library Manual).

```
C      D02BBF EXAMPLE PROGRAM TEXT
C      MARK 7 RELEASE. NAG COPYRIGHT 1978.
C      .. SCALARS IN COMMON ..
       REAL H, XEND
       INTEGER I
C      ..
C      .. LOCAL SCALARS ..
       REAL PI, TOL, X
       INTEGER IFAIL, IR, J, N, NOUT
C      .. LOCAL ARRAYS ..
       REAL W(3,7), Y(3)
C      .. FUNCTION REFERENCES ..
```

```
      REAL X01AAF
C     .. SUBROUTINE REFERENCES ..
C     D02BBF
C     ..
      EXTERNAL FCN, OUT
      COMMON XEND, H, I
      DATA NOUT /6/
      WRITE (NOUT,99996)
      PI = X01AAF(X)
      N = 3
      IR = 0
      DO 20 J=4,5
         TOL = 10.**(-J)
         WRITE (NOUT,99999) TOL
         WRITE (NOUT,99998)
         X = 0.
         XEND = 8.E0
         Y(1) = 0.E0
         Y(2) = 0.5E0
         Y(3) = 0.2E0*PI
         H = (XEND-X)/8.
         I = 7
         IFAIL = 1
         CALL D02BBF(X, XEND, N, Y, TOL, IR, FCN, OUT, W, IFAIL)
         WRITE (NOUT,99997) IFAIL
         IF (TOL.LT.0.) WRITE (NOUT,99995)
   20 CONTINUE
      STOP
99999 FORMAT (22H0CALCULATION WITH TOL=, E8.1)
99998 FORMAT (40H X AND SOLUTION AT EQUALLY SPACED POINTS)
99997 FORMAT (8H  IFAIL=, I1)
99996 FORMAT (4(1X/), 31H D02BBF EXAMPLE PROGRAM RESULTS/1X)
99995 FORMAT (24H RANGE TOO SHORT FOR TOL)
      END
      SUBROUTINE FCN(T, Y, F)
C     .. SCALAR ARGUMENTS ..
      REAL T
C     .. ARRAY ARGUMENTS ..
      REAL F(3), Y(3)
C     ..
C     .. FUNCTION REFERENCES ..
      REAL COS, SIN
C     ..
      F(1) = SIN(Y(3))/COS(Y(3))
      F(2) = -0.032E0*F(1)/Y(2) - 0.02E0*Y(2)/COS(Y(3))
      F(3) = -0.032E0/(Y(2)*Y(2))
      RETURN
      END
      SUBROUTINE OUT(X, Y)
C     .. SCALAR ARGUMENTS ..
      REAL X
C     .. ARRAY ARGUMENTS ..
      REAL Y(3)
C     ..
C     .. SCALARS IN COMMON ..
```

```
      REAL H, XEND
      INTEGER I
C     ..
C     .. LOCAL SCALARS ..
      INTEGER J, NOUT
C     ..
      COMMON XEND, H, I
      DATA NOUT /6/
      WRITE (NOUT,99999) X, (Y(J),J=1,3)
      X = XEND - FLOAT(I)*H
      I = I - 1
      RETURN
99999 FORMAT (1H , F7.2, 3E13.5)
      END
```

### 13.2. Program Data

None.

### 13.3. Program Results

```
 D02BBF EXAMPLE PROGRAM RESULTS

 CALCULATION WITH TOL= 0.1E-03
 X AND SOLUTION AT EQUALLY SPACED POINTS
    0.00  0.00000E+00  0.50000E+00  0.62832E+00
    1.00  0.62712E+00  0.44642E+00  0.48440E+00
    2.00  0.10493E+01  0.40548E+00  0.30662E+00
    3.00  0.12573E+01  0.38055E+00  0.97690g-01
    4.00  0.12422E+01  0.37433E+00 -0.12889E+00
    5.00  0.99494E+00  0.38731E+00 -0.35142E+00
    6.00  0.50556E+00  0.41730E+00 -0.55067E+00
    7.00 -0.23703E+00  0.46051E+00 -0.71789E+00
    8.00 -0.12458E+01  0.51298E+00 -0.85370E+00
  IFAIL=0
 CALCULATION WITH TOL= 0.1E-04
 X AND SOLUTION AT EQUALLY SPACED POINTS
    0.00  0.00000E+00  0.50000E+00  0.62832E+00
    1.00  0.62716E+00  0.44642E+00  0.48440E+00
    2.00  0.10493E+01  0.40548E+00  0.30662E+00
    3.00  0.12574E+01  0.38055E+00  0.97675E-01
    4.00  0.12423E+01  0.37433E+00 -0.12891E+00
    5.00  0.99497E+00  0.38731E+00 -0.35144E+00
    6.00  0.50554E+00  0.41731E+00 -0.55069E+00
    7.00 -0.23709E+00  0.46052E+00 -0.71791E+00
    8.00 -0.12459E+01  0.51299E+00 -0.85371E+00
  IFAIL=0
```